plant sciences

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VOLUME 1
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Preface

Someone once said that if you want to find an alien life form, just go into your backyard and grab the first green thing you see. Although plants evolved on Earth along with the rest of us, they really are about as different and strange and wonderful a group of creatures as one is likely to find anywhere in the universe.

The World of Plants

Consider for a minute just how different plants are. They have no mouths, no eyes or ears, no brain, no muscles. They stand still for their entire lives, planted in the soil like enormous drinking straws wicking gallon after gallon of water from the earth to the atmosphere. Plants live on little more than water, air, and sunshine and have mastered the trick of transmuting these simple things into almost everything they (and we) need. In this encyclopedia, readers will find out how plants accomplish this photosynthetic alchemy and learn about the extraordinary variety of form and function within the plant kingdom. In addition, readers will be able to trace their 450-million-year history and diversification, from the very first primitive land plants to the more than 250,000 species living today.

✶Explore further in Photosynthesis, Light Reactions and Evolution of Plants

All animals ultimately depend on photosynthesis for their food, and humans are no exception. Over the past ten thousand years, we have cultivated such an intimate relationship with a few species of grains that it is hardly an exaggeration to say, in the words of one scientist, that "humans domesticated wheat, and vice versa." With the help of agriculture, humans were transformed from a nomadic, hunting and gathering species numbering in the low millions, into the most dominant species on the planet, with a population that currently exceeds six billion. Agriculture has shaped human culture profoundly, and together the two have reshaped the planet. In this encyclopedia, readers can explore the history of agriculture, learn how it is practiced today, both conventionally and organically, and what the impact of it and other human activities has been on the land, the atmosphere, and the other creatures who share the planet with us.

✶Explore further in Agriculture, Modern and Human Impacts

Throughout history—even before the development of the modern scientific method—humans experimented with plants, finding the ones that provided the best meal, the strongest fiber, or the sweetest wine. Naming a thing is such a basic and powerful way of knowing it that all cultures have created some type of taxonomy for the plants they use. The scientific understanding of plants through experimentation, and the development of ra-

tional classification schemes based on evolution, has a rich history that is explored in detail in this encyclopedia. There are biographies of more than two dozen botanists who shaped our modern understanding, and essays on the history of physiology, ecology, taxonomy, and evolution. Across the spectrum of the botanical sciences, progress has accelerated in the last two decades, and a range of entries describe the still-changing understanding of evolutionary relationships, genetic control, and biodiversity.

✶Explore further in Ecology, History of; Biodiversity; and Phylogeny

With the development of our modern scientific society, a wide range of new careers has opened up for people interested in plant sciences, many of which are described in this encyclopedia. Most of these jobs require a college degree, and the better-paying ones often require advanced training. While all are centered around plants, they draw on skills that range from envisioning a landscape in one's imagination (landscape architect) to solving differential equations (an ecological modeler) to budgeting and personnel management (curator of a botanical garden).

✶Explore further in Curator of a Botanical Garden and Landscape Architect

Organization of the Material

Each of the 280 entries in *Plant Sciences* has been newly commissioned for this work. Our contributors are drawn from academic and research institutions, industry, and nonprofit organizations throughout North America. In many cases, the authors literally "wrote the book" on their subject, and all have brought their expertise to bear in writing authoritative, up-to-date entries that are nonetheless accessible to high school students. Almost every entry is illustrated and there are numerous photos, tables, boxes, and sidebars to enhance understanding. Unfamiliar terms are highlighted and defined in the margin. Most entries are followed by a list of related articles and a short reading list for readers seeking more information. Front and back matter include a geologic timescale, a topic outline that groups entries thematically, and a glossary. Each volume has its own index, and volume 4 contains a cumulative index covering the entire encyclopedia.

Acknowledgments and Thanks

I wish to thank the many people at Macmillan Reference USA and the Gale Group for their leadership in bringing this work to fruition, and their assiduous attention to the many details that make such a work possible. In particular, thanks to Hélène Potter, Brian Kinsey, Betz Des Chenes, and Diane Sawinski. The editorial board members—Robert Evans, Wendy Mechaber, and Robert Wallace—were outstanding, providing invaluable expertise and extraordinary hard work. Wendy is also my wife, and I wish to thank her for her support and encouragement throughout this project. My own love of plants began with three outstanding biology teachers, Marjorie Holland, James Howell, and Walt Tulecke, and I am in their debt. My many students at the Commonwealth School in Boston were also great teachers—their enthusiastic questions over the years deepened my own understanding and appreciation of the mysteries of the plant world. I hope that a new generation of students can discover some of the excitement and mystery of this world in *Plant Sciences.*

Richard Robinson
Editor in Chief

Geologic Timescale

<table>
<tr><th>Era</th><th colspan="2">Period</th><th>Epoch</th><th>started (millions of years ago)</th></tr>
<tr><td rowspan="7">Cenozoic
66.4 millions of years ago–present time</td><td colspan="2" rowspan="2">Quaternary</td><td>Holocene</td><td>0.01</td></tr>
<tr><td>Pleistocene</td><td>1.6</td></tr>
<tr><td rowspan="5">Tertiary</td><td rowspan="2">Neogene</td><td>Pliocene</td><td>5.3</td></tr>
<tr><td>Miocene</td><td>23.7</td></tr>
<tr><td rowspan="3">Paleogene</td><td>Oligocene</td><td>36.6</td></tr>
<tr><td>Eocene</td><td>57.8</td></tr>
<tr><td>Paleocene</td><td>66.4</td></tr>
<tr><td rowspan="8">Mesozoic
245–66.4 millions of years ago</td><td colspan="2" rowspan="2">Cretaceous</td><td>Late</td><td>97.5</td></tr>
<tr><td>Early</td><td>144</td></tr>
<tr><td colspan="2" rowspan="3">Jurassic</td><td>Late</td><td>163</td></tr>
<tr><td>Middle</td><td>187</td></tr>
<tr><td>Early</td><td>208</td></tr>
<tr><td colspan="2" rowspan="3">Triassic</td><td>Late</td><td>230</td></tr>
<tr><td>Middle</td><td>240</td></tr>
<tr><td>Early</td><td>245</td></tr>
<tr><td rowspan="15">Paleozoic
570–245 millions of years ago</td><td colspan="2" rowspan="2">Permian</td><td>Late</td><td>258</td></tr>
<tr><td>Early</td><td>286</td></tr>
<tr><td rowspan="2">Carboniferous</td><td>Pennsylvanian</td><td>Late</td><td>320</td></tr>
<tr><td>Mississippian</td><td>Early</td><td>360</td></tr>
<tr><td colspan="2" rowspan="3">Devonian</td><td>Late</td><td>374</td></tr>
<tr><td>Middle</td><td>387</td></tr>
<tr><td>Early</td><td>408</td></tr>
<tr><td colspan="2" rowspan="2">Silurian</td><td>Late</td><td>421</td></tr>
<tr><td>Early</td><td>438</td></tr>
<tr><td colspan="2" rowspan="3">Ordovician</td><td>Late</td><td>458</td></tr>
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<tr><td colspan="2" rowspan="3">Cambrian</td><td>Late</td><td>523</td></tr>
<tr><td>Middle</td><td>540</td></tr>
<tr><td>Early</td><td>570</td></tr>
<tr><td colspan="4">Precambrian time
4500–570 millions of years ago</td><td>4500</td></tr>
</table>

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VOLUME 1:

Absorption *See Water Movement.*

A

Acid Rain

Acid rain can be defined as rain that has a **pH** less than 5.6, formed primarily through the chemical transformation of sulfur and nitrogen **compounds** emitted by **anthropogenic** sources. In addition, acidic compounds can be deposited as aerosols and particulates (dry deposition), and mists, fogs, snow, and clouds (wet deposition). Most scientists agree that the phrase *acidic deposition* is more appropriate when characterizing the overall problem, but acid rain is the most widely used term.

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral; low pH numbers indicate high acidity; high numbers indicate alkalinity

compound a substance formed from two or more elements

anthropogenic human-made

Robert Angus Smith (1817–1884), a Scottish chemist, first used the expression "acid rain" in 1872 when describing the acidic nature of rain deposited around Manchester, England. The problem was believed to be localized and confined to urban areas until reports appeared during the 1970s and 1980s describing widespread acidification of lakes in the northeastern United States, eastern Canada, and Europe. Additional reports surfaced regarding declines in growth and vigor of forested **ecosystems** throughout the world, with acid rain as the possible culprit. These findings resulted in several large research initiatives, including the U.S. government-funded National Atmospheric Precipitation Assessment Program.

ecosystem an ecological community together with its environment

Results indicated that pH in rainfall, mists, clouds, snow, and fog in the United States, especially the East, was generally below normal, and was due to an increase in industrial emissions of sulfur and nitrogen compounds transported to rural areas. Some lakes and streams were acidified and their productivity reduced by acid rain. Most lakes and streams that were acidified were located in the northeastern United States. The majority of forested and agricultural ecosystems were found not to be directly affected by acid rain. Certain high-elevation systems, such as red spruce in the northeastern United States, were reported as possibly being affected by acid rain, but many other factors were involved. Research findings resulted in increased environmental legislation, including the 1990 Clean Air Act Amendments enacted by the U.S. Congress to significantly reduce sulfur emissions.

Since 1990, sulfur dioxide emissions have decreased 25 percent, resulting in a significant reduction in **sulfate** in rain and surface waters in some

sulfate a negatively charged particle combining sulfur and oxygen

A branch from a tree in Germany's Black Forest showing needle loss and yellowed boughs from acid rain (top) compared to a branch from a healthy tree (bottom).

areas of the United States. Nitrogen compounds, however, have not decreased. The role nitrogen plays in acidification is currently of concern to the scientific community. Several forested ecosystems have been found to be nitrogen **saturated**. Also, it is hypothesized that acid rain has caused a depletion in base **cations**, mainly calcium, potassium, and magnesium, in the soils of several forested ecosystems making uptake of these essential minerals more difficult. Research is underway to investigate the effects of these problems on ecosystem function. SEE ALSO Atmosphere and Plants.

Arthur H. Chappelka

saturated containing as much dissolved substance as possible

cations positively charged particles

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Agricultural Ecosystems

An agricultural ecosystem, which is also known as an agroecosystem, is a place where agricultural production—a farm, for example—is understood as an **ecosystem**. When something like a farm field is examined from an ecosystem viewpoint, food production can be understood as part of a whole, including the complex kinds of materials entering the system, or inputs, and the materials leaving the system, or outputs. At the same time, the ways that all of the parts of the system are interconnected and interact are of great importance.

ecosystem an ecological community together with its environment

Humans alter and manipulate ecosystems for the purpose of establishing agricultural production, and in the process, can make the resulting agroecosystem very different from a natural ecosystem. At the same time, however, by understanding how ecosystem processes, structures, and characteristics are modified, management of an agricultural system can become more stable, less dependent on inputs brought in from outside the system, and more protective of the natural resources with which it may interact.

Scientists who study agricultural systems as ecosystems are known as agroecologists, and the field they work in is known as agroecology. An agroecologist applies the concepts and principles of ecology to the design and management of sustainable agroecosystems. Sustainability refers to the ability to preserve the productivity of agricultural land over the long term, protect the natural resources upon which that productivity depends, provide farming communities with a fair and prosperous way of life, and produce a secure and healthy food supply for people who do not live on the farms. The challenge these scientists face is developing agroecosystems that achieve natural ecosystem-like characteristics while maintaining a harvest output. With a goal of sustainability, a farm manager strives as much as possible to use the ecosystem concept in designing and managing the agroecosystem. In doing so, the following four key traits of ecosystems are included.

Energy Flow

Energy flows into an ecosystem as a result of the capture of solar energy from the Sun by plants, and most of this energy is stored as **biomass** or used to maintain the internal processes of the system. But removing energy-rich biomass from the system causes changes. Human energy (considered renewable) as labor, and industrial energy (considered nonrenewable) from fossil fuels, become necessary. Agroecologists look for ways to increase the efficiency of the capture of energy from the Sun and increase the use of renewable energy, achieving a better balance between the energy needed to maintain internal processes and that which is needed for harvest export.

biomass the total dry weight of an organism or group of organisms

Nutrient Cycling

Many nutrients are cycled through ecosystems. Biomass is made up of organic **compounds** manufactured from these nutrients, and as organisms

compound a substance formed from two or more elements

Adjacent fields of rice and wheat in California's Sacramento Valley.

die and decompose, the nutrients return to the soil or the atmosphere to be recycled and reused again. Agricultural ecosystems lose nutrients with harvest removal, and because of their more simplified ecological structure, lose a greater proportion of nutrients to the air or by leaching in rain and irrigation water. Humans must return these nutrients in some form. In a well-designed agroecosystem, the farmer strives to keep nutrient cycles as closed as possible, reducing nutrient losses while searching for sustainable ways of returning exported nutrients to the farm.

Regulation of Populations

mutualism a symbiosis between two organisms in which both benefit

Complex interactions between organisms regulate their numbers in natural ecosystems. Competition, **mutualisms**, and other types of interactions are promoted by the organization and structure of the system. Growing one or very few crops in modern agriculture eliminates many of these interactions, often removing natural control mechanisms and allowing pest outbreaks. An agroecological alternative seeks to reintroduce more complex structures and species arrangements, often including both crop and noncrop species, in order to reduce the use of pesticides and enhance natural controls.

System Stability and Change

Ecosystems maintain themselves over time and have the ability to recover from natural disturbances such as a fire or a hurricane. In agricultural ecosystems, disturbance from cultivation, weeding, harvest, and other agricultural activities is much more intense and frequent. It is difficult to maintain any equilibrium in the system with this disturbance, requiring constant outside interference in the form of human labor and external human inputs. By incorporating ecosystem qualities such as diversity, stability, recovery, and balance, the maintenance of an ecological foundation for long-term sustainability can be established.

Agroecologists use the idea of an agricultural ecosystem as a focus for the study of farming systems that are converting from single crops and synthetic inputs to ecologically based design and management. Ecological concepts and principles are applied for the development of alternative practices and inputs. A good example is research done by Sean Swezey and his colleagues on apples in California. After three years of using organic farming techniques, an apple orchard had begun to show a reduction in the use of fossil fuel energy. Nutrients were supplied from compost and annual cover crops planted in the rows between the trees during the winter season. Nutrient recycling and storage in leaves and branches within the apple agroecosystem improved soil conditions, reduced the need for fertilizer, and even led to increased yields. Insect pests normally controlled by synthetic pesticides were reduced instead by beneficial predatory insects that were attracted to the organic orchard by mustard and fava-bean flowers in the rows between apple trees. Cover crop species smothered weeds so that herbicides were not needed. In the spring when the cover crop was mowed and cultivated into the soil, microorganism abundance and diversity increased, acting as a biological barrier to the outbreak of diseases in the soil. As the use of external human inputs for the control of the ecological processes in the apple system was reduced, a shift to the use of natural ecosystem processes and interactions and locally derived materials took place. Such an ecological foundation is an important way of determining the sustainability of the agricultural ecosystems of the future. SEE ALSO AGRICULTURE, MODERN; AGRICULTURE, ORGANIC; ECOSYSTEM.

Stephen R. Gliessman

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Agriculture, History of

The history of agriculture (the production of food by plant cultivation and animal husbandry and control of productivity) can be organized around

An ancient Egyptian fresco depicting a man harvesting wheat.

several themes (such as time, productivity, environmental impact, and genetic diversity). The most obvious is time and the sequence of events from gathering wild plants for food to crop plant **domestication**, to yield-enhanced **hybrid** seed.

domesticate to tame an organism to live with and to be of use to humans

hybrid a mix of two species

Origins of Agriculture

The origin of agriculture was around ten thousand years ago or approximately four hundred human generations back in time and prehistory, before written records were kept. What is known is based on evidence gathered from archaeological sites. Agriculture started independently in at least three places in the world, each with a distinctive cluster of plants drawn from the local flora: Mesoamerica (Mexico/Guatemala: corn, beans, squash, papaya, tomatoes, chili, peppers), the Fertile Crescent (Middle East from the Nile Valley to the Tigris and Euphrates Rivers: wheat, barley, grapes, apples, figs, melons, lentils, dates), and north China (mid-reaches of the three-thousand-mile-long Yellow River: rice, soybeans, peaches, Chinese cabbages such as bok choy). From these regions and possibly others, notably Africa (sorghum, cowpeas, yams, oil palm), South America (potatoes, sweet potatoes, cassava, peanuts, pineapples), and a broad band of tropical southeast Asia (oranges, mangoes, bananas, coconuts, sugarcane), the invention of agricultures spread to encompass the entire world by two thousand years ago.

The history of agriculture is not that of a single technology to produce food, but of an array of methodologies. Planting seed broadcast across plowed fields typifies most cereals (50 percent of human calories). Vegetables, **legumes**, and corn are planted from seed in rows separated by furrows. Seed agriculture usually consists of annuals that are typically planted as genetically uniform **monocultures**. Agriculture of the humid tropics has been more vegeculture than seed-based. These vegetatively **propagated** crops are usually perennials, productive over the entire year and found in **polycultures** that tend to mimic the forest **ecosystem**.

legumes beans and other members of the Fabaceae family

monoculture a large stand of a single crop species

propagate to create more of through sexual or asexual reproduction

polyculture mixed species

ecosystem an ecological community together with its environment

The earliest agriculture of southeast Asia was typically based on roots and tubers such as yams and taro, tree crops such as coconut and banana, and perennials such as sugarcane. In the Americas, vegeculture developed with cassava, sweet potatoes, arrowroot, and peanuts, and moved up the eastern slopes of the Andes, ultimately domesticating the potato. These crops spread quickly throughout the world after European contact. Potatoes displaced wheat and barley in cold soils of northern Europe and bananas became the fruit of choice in the New World tropics.

Seed agriculture dominates where either a pronounced dry season or a frost results in a single crop per year. In south China rice is the summer crop, sweet potato the winter crop. In India rice is the monsoon crop, wheat the winter crop. Sometimes intercropping (different crops in alternate rows) and relay planting (starting the next crop before the previous one is harvested) are part of the multiple-crops-per-year cycle. Sequential cropping is where one crop follows another without seasonal fallowing, sometimes in double-cropping but more often in triple-cropping.

Fallowing is an important technology perfected in the Middle Ages as part of the **crop rotation** pattern. The first year a legume is planted and the soil is enriched by the nitrogen-fixing crop; the next year a cereal is planted. The third year the land is rested to regain soil moisture and restore soil health. This pattern approximates a natural ecosystem and is more sustainable over the long term than continuous cropping. The fallow crop rotation system maximizes resources but is not elastic enough to accommodate an increasing human population that has come to rely on continuous cropping or heavy use of inputs (such as fertilizer, pesticides, and irrigation) in single crop per year monocultures.

crop rotation alternating crops from year to year in a particular field

Ecologic Effects

Another theme is to measure the displacement of natural ecosystems of forest and grasslands by plowed cropland that supports an increasing human population. Only about five million people existed worldwide preagriculture, subsisting on hunting and gathering of wild animals and plants. Humans existed like any other wild animals in the biological world. Postagriculture, the human population grew slowly, but as people's mastery of food production technology developed (such as irrigation, weed control by hoe and plow, and planting crops in monocultures) and the number of crop plants increased, the world population climbed to an estimated 130 million people by the time of Christ, a twenty-five-fold increase from the Paleolithic pre-agriculture estimate. By 1650 the world population had reached a half billion, and half of these people were in settled urbanized villages, towns, and cities and not engaged in agriculture to produce their own food. All of the major food crops and domestic farm animals known today were known and used worldwide. The only significant crops added since 1650 are industrial crops such as rubber.

Since the middle of the nineteenth century the population has increased from one billion to six billion, an increase that would not have been possible without increases in agricultural yields. Through breeding, plus the use of fossil fuels to plant, fertilize, and protect crops, the average yield of all plants and productivity per unit area has increased ten- to fiftyfold. At present humans produce and consume over a twenty-year period as much food as was produced in the eight thousand years between the development of agriculture and the sixteenth century. Nonetheless, of the six billion people in the world, over one billion are estimated to be malnourished, and half of these are seriously underfed, mostly due to poverty and the diminished affordability of agricultural products. An estimated fifty thousand to eighty thousand starve to death or are fatally compromised each day—a majority are children, in part because they are growing rapidly and do not get enough essential materials such as vitamin A or quality protein.

Loss of Diversity

Another theme is to realize how few crops currently feed the human population, considering that preagriculture humankind subsisted on a list of approximately five thousand wild edible plants. The agricultural crop list is short. One-half of the plant calories people consume come from three grasses: rice, wheat, and corn.

arable able to be cultivated for crops

Just over two dozen food plants account for 75 percent of all plant calories and 90 percent of **arable** land cultivated. This list includes six grasses: rice, wheat, corn, barley, oats, and sorghum; four legumes: soybeans, peanuts, common beans, and peas; two sugar crops: sugarcane and sugar beets; two tropical tree crops: bananas and coconuts; four starchy roots: potatoes, sweet potatoes, cassava, and yams; five fruits: tomatoes, grapes, apples, oranges, and mangoes; and two vegetables: cabbages and onions. These twenty-five crops literally stand between subsistence and starvation for the human population. This is an agricultural calorie list and does not recognize the extremely rich vitamin and mineral sources found in low-calorie vegetables and fruits. Also this list does not recognize the important regional foods of the world. For instance, the native American crop cranberries is extremely important to Americans at Thanksgiving but is insignificant on the world calorie chart (less than one-millionth of 1 percent).

Selection and Breeding

progenitors parents or ancestors

predation the act of preying upon; consuming for food

A dominant theme in the history of agriculture has been crop improvement and yield advancement through selection and exploitation of genetic diversity within the species and its close relatives. And now, there is bioengineering where a gene can come from anywhere in the biological world (genetically modified crops). The earliest stages of domesticated crops were probably not much more productive than the wild **progenitors**, but the act of cultivation and saving the seed to replant was a radical break with the past. Human selection (artificial selection) was replacing natural selection in shaping the plant. Traits associated with the domestication process are seeds and fruits that remain attached to the plant (nonbrittle rachis and nondehiscent fruits) and do not self sow. Another trait is larger fruits and seeds and less nondigestible fiber in seed coats and woody fibers (cellulose) in the fruits. This increases the palatability of these structures but leaves the plant less protected to insect or rodent **predation**, so that humans had to take greater care in postharvest storage. When humans planted the seed, they set in motion many selection forces that characterize domesticated plants: simultaneous and immediate germination on being sown in the ground; rapid and uniform growth; and a trend toward annuality if biennial/perennial. Additionally, a shortened vegetative phase often resulted in increased reproductive effort, thus increasing yield and uniform flowering and ripening. Most of these traits would be harmful for a wild plant.

Once domesticated plants began to travel through human migration and conquest beyond their local area of genetic adaptation, a large amount of genetic variation was released by chance **hybridization** of diverse forms or freedom from constraints (such as pests, **pathogens**, frost, and day length) of the old habitat. Citrus, for instance, was brought from East India to Spain by the Arabs, then taken to the West Indies by Europeans after Columbus. One mutant form gave rise to grapefruit, while a mutant orange in Brazil was the origin of the familiar navel orange.

hybridization formation of a new individual from parents of different species or varieties

pathogen disease-causing organism

The Columbian Exchange (New World plants to the Old World and vice versa) in the sixteenth century was the single most dramatic migration and acclimatization of crops throughout the world. Coupled with hybridization between dissimilar species, introductions of a tremendous number of new forms were generated. Examples are the potato from Peru, which conquered north Europe as a food plant displacing wheat/barley and turnips/peas; and tomatoes from Mexico, which were embraced in Italian cooking.

Recent yield improvement traces back to the rediscovery of Austrian botanist Gregor Mendel's (1822–1884) classic experiments on the heredity of garden peas. For the first time the plant breeding community had a set of principles by which to proceed with the crop improvement process. Products of this era are hybrid corn, changes in the **photoperiod** response of soybeans, and the dwarf-stature wheat from the International Center for the Improvement of Wheat and Corn (in Mexico) and rice from the International Rice Research Institute (in the Philippines). These late 1960s Green Revolution cereals and the genes they hold (dwarf stature and fertilizer responsive) now enter the food supply of three billion plus people and are directly responsible for feeding more than eight hundred million people by their increased yield alone. Never in world history had there been such a dramatic yield take-off as the Green Revolution. The hope is that the new and developing biotechnologies will have a comparable favorable outcome for global agriculture.

photoperiod the period in which an organism is exposed to light, or is sensitive to light exposure, causing flowering or other light-sensitive changes

landrace a variety or breed of plant

The irony of using elite improved varieties and commercial seed is that they have a tendency to eliminate the resources upon which they are based and from which they have been derived. Current elite varieties yield better than their parents and they displace them from farmers' fields. Once a displaced variety is no longer planted, its genes are lost to future generations unless it is conserved, usually in a seed bank collection or as a heirloom variety. The saving of old folk varieties, farmer **landraces** and garden seed passed down through a family, maintaining them in home gardens, has become increasingly widespread. Many of these heirloom varieties taste better, cook better, or possess other unique characteristics that set them apart, but they lack the productivity mechanized farming demands in modern agriculture. SEE ALSO AGRICULTURE, MODERN; AGRICULTURE, ORGANIC; AGRONOMIST; GREEN REVOLUTION; SEED PRESERVATION; SEEDS; VAVILOV, N. I.

Garrison Wilkes

Hybrid corn, a product of twentieth-century crop improvement processes.

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Agriculture, Modern

During the latter half of the twentieth century, what is known today as modern agriculture was very successful in meeting a growing demand for food by the world's population. Yields of primary crops such as rice and wheat increased dramatically, the price of food declined, the rate of increase in crop yields generally kept pace with population growth, and the number of people who consistently go hungry was slightly reduced. This boost in food production has been due mainly to scientific advances and new technologies, including the development of new crop varieties, the use of pesticides and fertilizers, and the construction of large irrigation systems.

Basic Practices of Modern Agricultural Systems

Modern agricultural systems have been developed with two related goals in mind: to obtain the highest yields possible and to get the highest economic profit possible. In pursuit of these goals, six basic practices have come to form the backbone of production: intensive tillage, **monoculture**, application of inorganic fertilizer, irrigation, chemical pest control, and genetic manipulation of crop plants. Each practice is used for its individual contribution to productivity, but when they are all combined in a farming system each depends on the others and reinforces the need for using the others. The work of agronomists, specialists in agricultural production, has been key to the development of these practices.

monoculture a large stand of a single crop species

Intensive Tillage. The soil is cultivated deeply, completely, and regularly in most modern agricultural systems, and a vast array of tractors and farm implements have been developed to facilitate this practice. The soil is loosened, water drains better, roots grow faster, and seeds can be planted more easily. Cultivation is also used to control weeds and work dead plant matter into the soil.

Monoculture. When one crop is grown alone in a field, it is called a monoculture. Monoculture makes it easier to cultivate, sow seed, control weeds, and harvest, as well as expand the size of the farm operation and improve aspects of profitability and cost. At the same time, monocultures tend to promote the use of the other five basic practices of modern agriculture.

Use of Synthetic Fertilizers. Very dramatic yield increases occur with the application of synthetic chemical fertilizers. Relatively easy to manufacture or mine, to transport, and to apply, fertilizer use has increased from five to ten times what it was at the end of World War II (1939–45). Applied in either liquid or granular form, fertilizer can supply crops with readily available and uniform amounts of several essential plant nutrients.

Fertilizer being applied to a rice field.

Irrigation Technologies. By supplying water to crops during times of dry weather or in places of the world where natural rainfall is not sufficient for growing most crops, irrigation has greatly boosted the food supply. Drawing water from underground wells, building reservoirs and distribution canals, and diverting rivers have improved yields and increased the area of available farm land. Special sprinklers, pumps, and drip systems have greatly improved the efficiency of water application as well.

Chemical Pest Control. In the large monoculture fields of much of modern agriculture, pests include such organisms as insects that eat plants, weeds that interfere with crop growth, and diseases that slow plant and animal development or even cause death. When used properly, synthetic chemicals have provided an effective, relatively easy way to provide such control. Chemical sprays can quickly respond to pest outbreaks.

Genetic Manipulation. Farmers have been choosing among crop plants and animals for specific characteristics for thousands of years. But modern agriculture has taken advantage of several more recent crop breeding techniques. The development of hybrid seed, where two or more strains of a crop are combined to produce a more productive offspring, has been one of the most significant strategies. Genetic engineering has begun to develop molecular techniques that selectively introduce genetic information from one organism to another, often times from very unrelated organisms, with a goal of capitalizing on specific useful traits.

But for almost every benefit of modern agriculture, there are usually problems. Excessive tillage led to soil degradation, the loss of organic matter, soil erosion by water and wind, and soil **compaction**. Large monocultures are especially prone to devastating pest outbreaks that often occur when pests encounter a large, uniform area of one crop species, requiring the continued and excessive use of chemical sprays. When used excessively, chemical fertilizers can be easily leached out of the soil into nearby streams and lakes, or even down into underground water supplies. Farmers can become dependent on chemical pest and weed control. Modern farm systems lack the natural control agents needed for biological pest management, and

compaction compacting of soil, leading to loss of air spaces larger amounts of sprays must be used as pests rapidly evolve resistance. People also worry about chemical pollution of the environment by sprays and fertilizers, and the possible contamination of food supplies. Modern agriculture has become such a large user of water resources that overuse, depletion, saltwater contamination, salt buildup in soil, fertilizer leaching, and soil erosion have become all too common. Agricultural water users compete with urban and industrial use, and wildlife as well. Hybrid seed has contributed greatly to the loss of genetic diversity and increased risk of massive crop failure, as well as an increased dependence on synthetic and nonrenewable inputs needed for maintaining high yield. Genetically engineered crops have the same negative potential, especially as the selection process takes place less and less in the hands of farmers working in their own fields, but rather in far away laboratories.

ecosystem an ecological community together with its environment

viable able to live or to function

In the future, in order to take advantage of new technologies and practices, farming systems will need to be viewed as **ecosystems**, or agricultural ecosystems. By monitoring both the positive and negative impacts of modern farming practices, ecologically based alternatives can be developed that protect the health of the soil, air, and water on farms and nearby areas, lower the economic costs of production, and promote **viable** farming communities around the world. Organic agriculture, conservation tillage, integrated pest management (IPM), and the use of appropriate genetic techniques that enhance local adaptation and variety performance are a few of the possible ways of ensuring the sustainability of future generations of farmers. SEE ALSO Agricultural Ecosystems; Agriculture, History of; Agriculture, Organic; Agronomist; Breeder; Breeding; Fertilizer; Herbicides.

Stephen R. Gliessman

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Agriculture, Organic

crop rotation alternating crops from year to year in a particular field

legumes beans and other members of the Fabaceae family

green manure crop planted to be plowed under, to nourish the soil, especially with nitrogen

tilth soil structure characterized by open air spaces and high water storage capacity, due to high levels of organic matter

monoculture a large stand of a single crop species

Organic farming is a production system that sustains agricultural productivity while avoiding or largely excluding synthetic fertilizers and pesticides. Whenever possible, external resources, such as commercially purchased chemicals and fuels, are replaced by resources found on or near the farm. These internal resources include solar or wind energy, biological pest controls, and biologically fixed nitrogen and other nutrients released from organic matter or from soil reserves. Thus organic farmers rely heavily on the use of **crop rotations**, crop residues, animal manures, compost, **legumes**, **green manures,** off-farm organic wastes, mechanical cultivation, mineral-bearing rocks, and aspects of biological pest control to maintain soil productivity and **tilth,** to supply plant nutrients, and to control insect pests, weeds, and diseases. In essence, organic farming aims to promote soil health as the key to sustaining productivity, and most organic practices are designed to improve the ability of the soil to support plant and microorganism life.

In contrast, conventional farming is characterized by **monoculture** systems that are heavily dependent on the use of synthetic fertilizers and pesticides. Although such systems are productive and able to furnish low-cost food, they also often bring a variety of environmental effects such as pesticide pollution, soil erosion, water depletion, and biodiversity reduction. Increasingly, scientists, farmers, and the public in general have questioned the sustainability of modern agrochemically based agriculture. A large number of organic farmers do use modern machinery, recommended crop varieties, certified seed, sound livestock management, recommended soil and water conservation practices, and innovative methods of organic waste recycling and residue management. Clearly, though, there are sharp contrasts between organic and conventional agriculture.

Most management systems used by organic farmers feature legume-based rotations, the application of compost, and several diversified cropping systems, including crop-livestock mixtures. Through the adoption of such practices, organic farmers aim at:

- building up soil organic matter and soil **biota**
- minimizing pest, disease, and weed damage
- conserving soil, water, and biodiversity resources
- long-term agricultural productivity
- optimal nutritional value and quality of produce
- creating an aesthetically pleasing environment.

biota the sum total of living organisms in a region of a given size

Features of Organic Farming

Organic farming is widespread throughout the world and is growing rapidly. In Germany alone there are about eight thousand organic farms occupying about 2 percent of the total **arable** land. In Italy organic farms number around eighteen thousand, and in Austria about twenty thousand organic farms account for 10 percent of total agricultural output. In 1980 the U.S. Department of Agriculture (USDA) estimated that there were at least eleven thousand organic farms in the United States and at least twenty-four thousand farms that use some organic techniques. In California, organic foods are one of the fastest-growing segments of the agricultural economy, with retail sales growing at 20 percent to 25 percent per year. Cuba was the only country undergoing a massive conversion to organic farming, promoted by the drop of fertilizer, pesticide, and petroleum imports after the collapse of trade relations with the Soviet bloc in 1990.

arable able to be cultivated for crops

Parasitic encarsia wasps are introduced to the foliage of a South African 'Yellow Trumpet' (*Phygelius aequalis* 'Yellow Trumpet') in order to combat whitefly at the botanical gardens in Swansea, Wales.

Given new market opportunities, farmers grow all kinds of crops, including field, horticultural, and specialty crops, as well as fruits and animals such as cattle, pigs, poultry, and sheep.

Although research on organic farming systems was very limited until the early 1980s, pioneering studies of R. C. Oelhaf (1978), the USDA (1980), W. Lockeretz and others (1981), D. Pimentel and others (1983), and the National Research Council (1984) on organic farming in the United States provide the most comprehensive assessments of organic agricultural systems. These studies concluded the following:

1. As farmers convert to organic farming, initially crop yields are lower than those achieved in conventional farms. In the corn belt, corn yields were about 10 percent less and soybean yields were about 5 percent less on organic farms than on paired conventional farms. Un-

DISTINGUISHING CHARACTERISTICS OF CONVENTIONAL AND ORGANIC FARMING

Characteristics	Conventional	Organic
Petroleum dependency	High	Medium
Labor requirements	Low, hired	Medium, family or hired
Management intensity	High	Low–medium
Intensity of tillage	High	Medium
Plant diversity	Low	Medium
Crop varieties	Hybrids	Hybrid or open pollinated
Source of seeds	All purchased	Purchased, some saved
Integration of crops and livestock	None	Little (use of manure)
Insect pests	Very unpredictable	Unpredictable
Insect management	Chemical	Integrated pest management, biopesticides, some biocontrol
Weed management	Chemical, tillage	Cultural control
Disease management	Chemical, vertical resistance	Antagonists, horizontal resistance, multiline cultivars
Plant nutrition	Chemical, fertilizers applied in pulses, open systems	Microbial biofertilizers, organic fertilizers, semi-open systems
Water management	Large-scale irrigation	Sprinkler and drip irrigation

der highly favorable growing conditions, conventional yields were considerably greater than those on the organic farms. Under drier conditions, however, the organic farmers did as well or better than their conventional neighbors. Beyond the third or fourth year after conversion and after crop rotations became established, organic farm yields began to increase, so that their yields approached those obtained by conventional methods.

2. Conventional farms consumed considerably more energy than organic farms largely because they used more petrochemicals. Also, organic farms were considerably more energy-efficient than conventional farms. Between 1974 and 1978 the energy consumed to produce a dollar's worth of crop on organic farms was only about 40 percent as great as on conventional farms.

3. Studies conducted in the Midwest between 1974 and 1977 found that the average net returns of organic and conventional farms were within 4 percent of each other. Organic farms had a lower gross income by 6 percent to 13 percent, but their operating costs were less by a similar amount.

4. The USDA formulated Midwest farm budgets in order to compare crop rotations on organic farms with continuous conventional crop practices. The analysis assumed that yields on organic farms were 10 percent lower. In addition, rotations tie up part of the cropland with forage legumes, such as alfalfa; on conventional farms this land would be producing either corn or soybeans. Since corn and soybeans command a higher price, potential income is reduced in proportion to the amount of land tied up in forage legumes. In essence, organic farmers are turning part of their potential income into renewal of the soil (by adding organic matter) in order to assure sustainability of future crop production. The conventional system maximizes present income and is not as concerned about viewing soil as a long-term investment. In conclusion, although initially yields are likely to be lower in organic farms, variable costs are likely to be much lower. With lit-

tle or no expenditure on agrochemicals, and the availability of premium prices for certain crops, the net result may be similar or higher gross margins for organic farmers.

5. Many organic farms are highly mechanized and use only slightly more labor than conventional farms. When based on the value of the crop produced, however, 11 percent more labor was required on the organic farms because the crop output was lower. The labor requirements of organic farmers in this study were similar to those of conventional farmers for corn and small grains, but higher for soybeans because more hand weeding was necessary. A number of other studies indicated that organic farms generally require more labor than conventional farms, but such needs can be kept to a minimum if hand weeding or handpicking of insects is not used. The labor required to farm organically is a major limitation to the expansion of some organic farms and an important deterrent for conventional farmers who might consider shifting to organic methods.

In many ways, organic farming conserves natural resources and protects the environment more than conventional farming. Research shows that soil erosion rates are lower in organic farms, and that levels of biodiversity are higher in organic farming systems than in conventional ones. In addition, organic farming techniques tend to conserve nitrogen in the soil/plant system, often resulting in a buildup of soil organic nitrogen. Organically managed soils have more soil microorganisms and enhanced levels of potentially available soil nitrogen.

Conversion to Organic Farming

In order for farmers to become certified organic producers, they must complete a certification procedure. The United States and most European countries have created regulations that apply to the production and sale of organically grown produce. All organic produce must carry a quality mark authorized by the government and provided to farmers by legal organizations that conduct strong verification systems with on-site annual inspections. Farmers willing to convert to organic farming must adhere to specific production standards and can be certified as organic only after three years of strictly following such standards.

From a management perspective, the process of conversion from a high-input conventional management to a low-input (or low-external input) management is a transitional process with four marked phases:

1. Progressive chemical withdrawal
2. Rationalization of agrochemical use through integrated pest management (IPM) and integrated nutrient management
3. Input substitution, using alternative, low-energy inputs
4. Redesign of diversified farming systems with an optimal crop/animal assemblage so that the system can support its own soil fertility, natural pest regulation, and crop productivity.

During the four phases, management is guided in order to ensure the following processes:

1. Increasing biodiversity both in the soil and aboveground

biomass the total dry weight of an organism or group of organisms

2. Increasing **biomass** production and soil organic matter content
3. Decreasing levels of pesticide residues and losses of nutrients and water
4. Establishment of functional relationships between the various farm components
5. Optimal planning of crop sequences and combinations and efficient use of locally available resources.

It is important to note that the conversion process can take anywhere from one to five years depending on the level of artificialization or degradation of the original high-input system. In addition, not all input substitution approaches are ecologically sound, as it is well established that some practices widely encouraged by some organic farming enthusiasts (such as flame-weeding and applications of broad spectrum insecticides) can have serious side effects and environmental impacts.

For scientists involved in transition research, an important outcome of these studies is the realization that the process of converting a conventional crop production system that relies heavily on synthetic, petroleum-based inputs to a legally certifiable, low-external input, organic system is not merely a process of withdrawing external inputs, with no compensatory replacement or alternative management. Considerable ecological knowledge is required to direct the array of natural flows necessary to sustain yields in a low-input system. SEE ALSO Agricultural Ecosystems; Agriculture, History of; Agriculture, Modern; Agronomist; Compost; Soil, Chemistry of; Soil, Physical Characteristics of.

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Agronomist

Agronomy is the branch of agriculture and biology that explores the principles and concepts of plants and soils sciences. It also examines manage-

Agronomists place a plastic greenhouse over crops that will be exposed to simulated rain with varying pH levels, allowing the scientists to assess the plants' reaction to the rain.

ment practices designed to optimize production for the benefit of humankind while protecting nature's resources. Agronomy is derived from the Greek words *agros* (field) and *nomos* (to manage).

Agronomy has been recognized as a separate and distinct branch of agriculture since the early 1900s, when departments of agriculture at **land-grant universities** were split into animal science and agronomy units. In 1900 agronomy units included crop science, soil science, farm management (agricultural economics), and agricultural engineering. In the 1920s and 1930s separate departments of agricultural economics, agricultural engineering, crop science, and soil science emerged. This trend to create specialized departments at the college or university level has resulted in less use of the term *agronomy;* however, it certainly has not diminished the meaning of or demand for resource managers charged with the responsibility of protecting and utilizing land, water, and plants for the benefit of humankind.

land-grant university a state university given land by the federal government on the condition that it offer courses in agriculture

Diversity of Activities and Career Fields

Agronomy is an amalgamation of many narrowly defined disciplines or specializations focused on providing the practicing agronomist with the knowledge and understanding to make management decisions that increase productivity, utilize resources most efficiently, protect the environment, and serve society. Agronomy reflects a combination of laboratory, field, and processing activities.

Throughout the twentieth century shifts in member interests resulted in the emergence of new specializations or subdisciplines. Many reflect areas of research requiring advance study or graduate degrees. Agronomists have become renewable resource managers, particularly in the area of highly important commercial farming activities where optimizing production using new, cost-effective technology is key. Agronomists also manage various kinds of landscapes and the vegetation occupying them for direct use by humans, the support of livestock and wildlife, development of water resources, and for aesthetic, recreational, and military uses.

Agronomists at the bachelor's level find about 60 percent employment in the private sector and 30 percent in the public sector (10 percent pursue graduate studies). Graduate-level employment is approximately 65 percent in the public sector and 35 percent in the private sector. SEE ALSO Agriculture, Modern; Agriculture, Organic.

Vernon B. Cardwell

Alcoholic Beverage Industry

Wine

Wine has been made by humans for over eight thousand years. First made from wild grapes, today wine is produced from grapevines grown in cultivated vineyards. Vineyards produce not only wine grapes but fresh table grapes and raisins for eating as well. It takes the scientific knowledge and artistic craftsmanship of a well-educated vineyard manager and wine maker to create the finest wines.

The way wine smells and tastes depends on the grapes from which it is made, the alcoholic fermentation, and the processing and aging of the new wine. At harvest, wine makers have the following responsibilities: deciding when to pick the grapes, scheduling delivery to the winery, overseeing crushing and pressing, and monitoring the fermentations. After fermentation, wine makers must choose from the many options to finish a young wine. They supervise the winery staff to complete the different wine processing steps, such as the transfer of the wine to other vessels (racking), clarification (fining), filtration, blending of different-flavored wines, and bottling. They are responsible for assuring wine quality by sampling, tasting, and chemical analysis. Production and sale of alcoholic beverages is strictly regulated by the state and federal governments, and wine makers must keep accurate records of the wine produced to ensure that the winery complies with these regulations.

Vineyard managers direct the harvest operations by guiding the vineyard crew and harvest workers. The managers are responsible for making decisions about new plantings, the support structure (trellis) for new vines, as well as their pruning after harvest. The managers prepare schedules for water and fertilizer application, control vine pests and diseases, oversee vineyard experiments, and coordinate the sampling of grapes in the vineyard to determine ripeness prior to harvest.

While there is no official certification for wine makers or vineyard managers, students majoring in viticulture and enology (the science and tech-

A vintner at the Joseph Drouhin Winery in Vosne-Romanée, France, fills a wooden vat with red Burgundy grapes.

nology of grape growing and wine making) must develop both broad theoretical skills and in-depth technical knowledge, as well as excellent communication and problem-solving skills. Both prospective wine makers and vineyard managers need a comprehensive preparation in plant biology and microbiology, mathematics and statistics, chemistry, biochemistry, and physics. College course work focuses on the underlying scientific principles so that the students can understand current wine industry practices. These students are required to take an array of specialized courses on such subjects as vineyard establishment and management, grape development and composition, wine sensory evaluation and instrumental analysis, and winery design, as well as management, marketing, and economics. By taking local and overseas internships, students obtain valuable real-world experience from practicing enologists and viticulturists, and critically apply their understanding to create their own innovative styles and practices.

In the Northern Hemisphere, the grape harvest (crush) occurs usually between the end of August and the beginning of November, depending on location, grape variety, and weather. Intense, physically demanding fourteen-hour days (seven days a week) are to be expected during the peak of crush.

In the off-season, wine makers have become increasingly involved in the business aspects of the winery, which means they enjoy a significant amount of traveling to promote their wines, as well as public speaking and other marketing activities. The vineyard manager attends to the vines year-round and is in constant communication with the vineyard crew and the wine maker to ensure the best grape quality and yield.

As wine makers and vineyard managers deal with the production of an alcoholic beverage, they serve as role models to coworkers and consumers, educating them about the responsibilities and consequences associated with its consumption. Winegrowers enjoy teaching an appreciation for the challenges of growing an agricultural crop, good stewardship of their farmland, and respect for the great technical and artistic challenges to create a beverage that is highly regarded worldwide.

Today, wine grapes are grown in countries with moderate climates around the world, often in scenic places, especially along coastal valleys and major rivers. Living in a beautiful environment and being able to taste the fruit of one's labor are among the most rewarding aspects of becoming a successful, and sometimes famous, wine maker or grape grower. This greatly compensates for the intense seasonal workload during harvesttime and a relatively modest starting salary. The annual salary depends a lot on the size of the winery. In 1999 the average salary was $28,000 to $64,000 for assistant wine makers, $49,000 to $112,000 for wine makers, and $37,000 to $64,000 for vineyard managers. Starting salaries were around $25,000 for qualified graduates with a bachelor's degree to $35,000 for those with a master of science degree.

Beer

Beer was probably first made by the Egyptians at least five thousand years ago, possibly as a variation of baking. There is considerable evidence of beer being used in religious rituals, for sacrifice, and also in medicines. Beer is made from malt that, in turn, is made from barley. Barley is steeped (soaked) in water and then permitted to germinate with constant turning and **aeration** for four to five days. It is then dried and heated (kilned), which imparts the delicious flavors of malt. In the brewery, malt is milled and mixed with hot water (known as mashing), which extracts the starch in the form of sugars. This "wort" is then boiled with hops to add bitterness. After cooling, yeast is added and fermentation creates alcohol and carbon dioxide and a myriad of desirable flavor **compounds**. After aging to clarify and stabilize the beer, it is packaged and pasteurized for sale.

aeration introduction of air

compound a substance formed from two or more elements

The malt beverage industry comprises three interdependent industries: brewing, malting, and hop supply. Although some brewers grow hops and make malt, the malt and hop industries are generally independent. These industries are dominated by a few giant companies who have an international reach.

The malt and hop industries employ students trained in plant sciences because these businesses grow, store, and use living plants. Employees must maintain good working relations with growers of barley and hops and advise them as well to assure that malting barley is planted and nurtured correctly. Superior barley is selected and purchased upon harvest. The storage and manufacture of malt or hop products, their analysis and processing to

Employees at the Carlsberg Brewery in Copenhagen, Denmark, use computers to monitor the beer-making process as tourists look down on the vats where the beer is made.

a final product, and research and sales, also tend to involve plant scientists although a broader range of skills, including chemistry and engineering, are required. Finally the malt and hop industries maintain cordial relations with the brewers through technical sales and services.

Professional employees of these industries are therefore in the field with farmers, in the processing plants, in the analytical laboratory, or on the road visiting customers. Good communications skills are necessary. Such employees in these industries are relatively few, and there are no large pyramidal management structures for steady upward mobility and advancement over many years. Experienced employees, however, are valued and well compensated, because they build important relationships with growers and customers. Entry salaries tend to be modest although good for the sometimes rural locations of the work.

Barley for malting tends to be grown close to the Canadian border, from Minnesota to Washington, where the malt houses (factories) for making malt are also located. Hop growing and processing is concentrated in the Pacific Northwest.

Brewing companies are much less likely to seek plant scientists for employment. They tend to seek graduates in food science, food engineering, or chemical engineering. For specific tasks of laboratory analysis, those with experience in chemistry or microbiology might be required. The reason is that by the time the malt and hop products reach the brewery they have lost their identity as plant materials and are now simply bulk **commodities** with specified properties for the process of making beer.

commodities goods that are traded, especially agricultural goods

Brewers work in large plants operating sophisticated machinery in which huge volumes of a highly perishable product are processed. Much of the work is computerized. Brewers are dedicated to following well-established operating procedures for consistent production of a high-quality product in the brew house, fermenting and aging cellars, and packaging plant, as well as using standard methods in the laboratory for analysis of the product.

There are no specific training programs for the malting and hop industries; programs in cereal science and plant science, however, are broadly applicable to the field. Similarly, training in brewing science is restricted to one university, the University of California at Davis. SEE ALSO Agronomist; Alcoholic Beverages; Economic Importance of Plants; Food Scientist.

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Alcoholic Beverages

anaerobic without oxygen

Alcoholic beverages all share the common feature of being produced through **anaerobic** fermentation of plant-derived carbohydrate materials by yeasts. Sugars are converted to alcohol (ethanol) and carbon dioxide by these fungi, which also impart characteristic flavors and aromas to the beverage. Depending upon what fermentable material is used, and the method by which the materials are processed, alcoholic beverages may be classified as being wines, beers, or spirits. Many countries in which they are produced regulate the production of most spirits, beer, and wine and carefully control taxation of these alcoholic beverages.

Wine

Wines are alcoholic beverages that have been fermented from fleshy fruits (e.g., apples, grapes, peaches, and plums), although most often from the cultivated grape *Vitis vinifera* (family Vitaceae) and related species. While the vast majority of wines are made from grapes, wines may also be made from the vegetative parts of certain plants.

Wines are made by harvesting ripened grapes from farms known as vineyards. The timing of the harvest is critical, since a balance of accumulated sugar, acids, and other grape flavor components reaches an optimal level to ultimately produce a fine wine. If the grapes are harvested too soon or too late, there is the possibility of producing a lower quality wine. Bunches of

DISTINGUISHING CHARACTERISTICS OF ALCOHOLIC BEVERAGES

Beverage	Fermented Materials	Carbonated?	Distilled?	Other Features
Beers				
Ales	Barley malt, wheat, rice	Yes	No	Warm fermented
Stout	Highly kilned (dark) malt	Yes	No	An ale using dark malts
Lagers	Barley malt	Yes	No	Cold fermented
Weizen beers	Wheat malt	Yes	No	Wheat beers of Germany
Wines				
Red	Grapes fermented with skins	No	No	Served at room temperature
White	Grapes fermented without skins	No	No	Served chilled
Port	Grapes	No	No/Yes	Fortified with alcohol/ cognac
Champagne	Grapes fermented without skins	Yes	No	A sparkling wine
Sparkling wines	Grapes	Yes	No	May be blended
Spirits				
Whiskeys				
Scotch (single malt)	Barley malt, often peat-smoked	No	Yes	Aged in oak casks
Rye	Rye (at least 51 percent)	No	Yes	Maximum 80 proof
Bourbon	Corn (at least 51 percent)	No	Yes	Sour mashed with bacteria
Gin	Malt, other grains	No	Yes	Flavored with juniper cones
Rum	Sugarcane or molasses	No	Yes	Light or dark rums available
Tequila/Mescal	*Agave tequiliana* stems	No	Yes	Traditional drinks of Mexico
Vodka	Malt, grains, potatoes	No	Yes	Few additional flavors
Brandy/Cognac	Wines	No	Yes	Distilled wines
Liqueurs	Wines	No	Yes	Sweetened with added sugars
Other				
Sake	Rice	No	No	Double fermentation
Cider	Apples	Yes/No	No	May be flavored/spiced
Mead	Honey	Yes/No	No	May be flavored/spiced

grapes are removed from the vines, usually by manual labor, and are brought to the winery for production. The grapes are passed through a mechanical destemmer that removes the nonfruit portions of the bunches, and the fruits are then crushed to express the juice from the fleshy berries. The liquid obtained from the crushed grapes is termed "must." The must is placed in either open or closed fermentation vessels (typically closed vessels in modern wineries) and readied for fermentation. If red wines are being made, the skins from the pressed grapes are also added to the fermentation vessel (the grape skins contribute reddish pigments to the finished wine); for white wine production, the skins are not used and only clear must is fermented.

The must that is ready to be fermented is then inoculated with a particular strain of yeast (*Saccharomyces cerevisiae*) that has been selected for wine fermentation. There are hundreds of different strains of wine yeast, each imparting a particular flavor during the fermentation. When complete, the fermentation will produce an alcohol content of approximately 12 to 14 percent alcohol by volume. Following fermentation, any suspended particulate material (the lees) is allowed to settle, and the clear wine is siphoned (or racked) to a new storage vessel, which is usually a large barrel made from white oak wood. The wine is then conditioned in these barrels for a year or more, occasionally being racked to new oak barrels as the wine matures. Under these conditions, chemical reactions take place in the wine that add complexity to the flavor profile. Even contact with **tannins** in the walls of the barrel provides subtle and desirable flavor characteristics that lower quality wines conditioned in stainless steel vessels lack. Most wines are "still" (not carbonated), but sparkling wines are allowed to undergo another fermentation after they mature, and are bottled while this fermentation is occuring, thereby carbonating the wine. Champagne is one famous version of a sparkling (white) wine originally from the region of France known by that name.

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

Wines are bottled in glass containers and are usually sealed by inserting a compressed cork into the neck of the bottles. Wine is stored and further matured while laying on the side, so that the cork remains moist to maintain its airtight seal. Some wines should be consumed within a year or two of production; others need many years or decades to achieve their optimum flavor.

The wine industry is an extensive one, with major centers of production in France, California, Italy, Spain, and Germany, with additional developing centers of production in South Africa, Australia, Argentina, and Chile. Although wine is vinted around the world, certain places are favored for wine production due to optimal climates and suitable land for the establishment of vineyards. Wine grapes often need warm days and cool nights, with minimal temperature extremes seasonally. Furthermore, ample sunlight, available soil nutrients, and sufficient water are required for grape production. Due to variation in seasonal climates, growing and harvest conditions, and seasonal timing of production events, significant changes occur from year to year that make wines produced in certain years of higher or lower quality. Thus, the practice of labeling vintages of wine (the year of wine production) and the grape variety from which they were made is established so that enologists (people who study wine) can evaluate differences from year to year, as well as to ensure that enophiles (people who enjoy and collect wine) can purchase wines of known quality. Since many of the variables that go into wine production are not controllable by the wine producers, differences are bound to occur in each production cycle. The variation in wine flavors is therefore unending and the source of fascination for many who appreciate wine.

Beer

Among the oldest records of the production and use of alcoholic beverages is that of beer, which originated in Mesopotamia and the Babylonian regions of Asia at least fifty-five hundred years ago. Beer is a beverage obtained by fermenting carbohydrate-containing extracts of various grains with yeast. It is usually flavored with bittering substances to balance the sweet flavor of unfermented sugars, which are typically found in beer.

The brewing process begins by taking grains, usually barley (*Hordeum vulgare*), and producing malt. To do this, viable barley grains are steeped in water and allowed to germinate under controlled conditions. The germination process produces **enzymes** that begin to break down the complex car-

enzyme a protein that controls a reaction in a cell

bohydrates (starch) found in the **endosperm** of the barley grains into soluble sugars. When a specified stage of germination is reached, the enzyme concentration in the sprouted grains is maximized to an optimal level, and the entire process is halted abruptly by rapid drying (called kilning) of the grains to remove most of the water. At this stage the sprouted and dried grains are called malt. The degree of kilning of the malt determines the darkness and color of the resulting beer; for instance, malts that are highly kilned produce beers with darker color.

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

In order to extract a sufficient amount of fermentable sugars, the malt is crushed to expose the embryo and endosperm components; the ground malt is called grist. To begin conversion of starches and complex carbohydrates into fermentable sugars, the grist is mixed with water (the mash) and heated to a temperature of approximately 65°C (150°F). Under these conditions, the once active enzymes (amylases) are reactivated and continue to break down the carbohydrate materials. When the brewer determines that the conversion is complete, the fluid portions of the mash are removed through a process known as sparging, and the liquid (called sweet wort) is transferred to a boiling vessel.

The sweet wort is then boiled for a specific length of time, typically one to two hours, while the resinous, cone-like **inflorescences** of the hop plant (*Humulus lupulus;* family Cannabinaceae) are added to provide flavoring, aromatic, and bittering characteristics to the beer. Hops contain resins, collectively termed lupulin, which gives the beer its characteristic aroma and bitterness. Prior to the use of hops, other herbs, such as spruce, nettle, and woodruff were used for the same purpose: to balance the beer's sweetness with bitterness. The boiling process also kills microorganisms that would otherwise spoil the wort, or produce undesirable fermentation products. The liquid that has been boiled with hops is now termed bitter wort; it is rapidly cooled and passed on to a fermentation vessel.

inflorescence an arrangement of flowers on a stalk

Fermentation historically took place in open-topped fermenters, although modern commercial breweries use closed fermenters and are meticulous in their sanitary practices to ensure that fermentation is accomplished only by the yeast strain with which the brewer inoculates the cooled bitter wort. Two main kinds of yeast are used: ales are beers fermented with beer strains of the yeast *Saccharomyces cerevisiae* at temperatures of 15° to 25°C (59° to 77°F); lagers are beers fermented with strains of *S. uvarum* at temperatures of 5° to 15°C (41° to 59°F), which are further conditioned (lagered) at near-freezing temperatures for several weeks or months. The alcohol content of the majority of beers is generally around 5 percent by volume, although certain styles of beer are produced with alcohol contents ranging from 8 to 14 percent and higher.

Some beers are naturally carbonated by continued slow fermentation after they are bottled, or they are artificially carbonated prior to bottling. Beers are also packaged in kegs (traditionally in oaken barrels) or in metal cans. Although the earliest beer production took place originally in the Middle East, the origins of modern beer styles can be traced to Germany, the United Kingdom, and the Czech Republic. There are a number of indigenous beers produced by many cultures around the world, but few have had as much influence on the brewing industry as those originating from the European region.

Spirits

Beverages produced from plant products that have been fermented and then distilled are considered spirits. The distillation process takes the fermented materials, often with a maximum alcohol content of 14 to 16 percent, and increases it to 40 to 75 percent alcohol by vaporizing the alcohol and many flavor components and then condensing them in specialized equipment known as stills. The concentrated alcoholic beverages resulting from this process are spirits or liquor, alluding to the condensate coming from the distillation process. Whiskeys (including Scotch or single-malt whiskey), bourbon, gin, vodka, rum, brandy, and various other liqueurs are produced through the distillation process. Each begins with a different starting material prior to fermentation and these impart different flavor characteristics in the finished spirit. Spirits are measured for alcohol content, and are then described as having a certain proof, or twice the measured alcohol content (an 86 proof whiskey has an alcohol content of 43 percent, for example). Spirits are the major component of mixed drinks.

Other Alcoholic Beverages

A variety of other alcoholic beverages exist in nearly every culture. Often they are safer to drink than local water sources, which may contain parasites, so they are widely used. Additionally, many alcoholic beverages complement different cuisines of served foods, and in some cases have been shown to improve digestion. Sake is a beerlike beverage originating in Japan that uses rice as the source of carbohydrate materials and is double fermented using yeast and a species of *Aspergillus* fungus. Cider (sometimes called hard cider) is an alcoholic beverage, popular in England, produced from yeast-fermented apple juice; it is occasionally flavored with a variety of spices. Mead, a beverage originating from medieval Europe, consists of honey that is fermented, occasionally together with other herbs or fruits, to produce a winelike drink that may be still or sparkling. The term "honeymoon" is coined from the practice of giving a gift of mead to a newly married couple: if they drank mead (honey) each night until the next moon, they would be given the gift of a new child. SEE ALSO Alcoholic Beverage Industry; Cork; Economic Importance of Plants; Grasses.

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Algae

Scientists' concepts of which organisms should be termed *algae* (alga, singular; algae, plural; algal, adjective) have changed radically over the past two centuries. The term algae originally referred to almost all aquatic, photosynthetic organisms. But, as more has been learned about the evolutionary

EUKARYOTIC ALGAE

Division	Common Name	Pigments	Habitats	General Morphology
Glaucophyta		Chlorophyll *a* Phycocyanin	Freshwater	Unicellular flagellates
Rhodophyta	Red algae	Chlorophyll *a* Phycoerythrin Phycocyanin	Mostly marine	Unicells, filaments, thalli; no flagellated stages; some calcified, some mucilaginous
Cryptophyta	Cryptomonads	Chlorophyll *a* Chlorophyll *c* Phycocyanin Phycoerythrin	Marine and freshwater	Mostly unicells
Heterokontophyta (Ochrophyta)				
Chrysophyceae	Golden brown algae	Chlorophyll *a* Chlorophyll *c* Fucoxanthin	Freshwater	Mostly unicells or colonies; biflagellate
Xanthophyceae (Tribophyceae)		Chlorophyll *a* Chlorophyll *c*	Mostly freshwater and terrestrial; some marine	Coccoid, flagellate, or amoeboid unicells; colonies, uni- and multinucleate filaments; biflagellate
Eustigmatophyceae		Chlorophyll *a* Violaxanthin	Freshwater and marine	Unicells and coccoid; uni- or biflagellate
Bacillariophyceae	Diatoms	Chlorophyll *a* Chlorophyll *c* Fucoxanthin	Freshwater and marine	Unicells and colonial coccoids; no flagella
Raphidophyceae		Chlorophyll *a* Chlorophyll *c* Fucoxanthin Diadinoxanthin Vaucheriaxanthin Heteroxanthin	Freshwater and marine (Marine species only)	Unicellular biflagellates
Dictyochophyceae	Silicoflagellates	Chlorophyll *a* Chlorophyll *c* Fucoxanthin	Marine	Unicellular uniflagellates
Phaeophyceae	Brown algae	Chlorophyll *a* Chlorophyll *c* Fucoxanthin	Marine	Multicellular; reproductive cells biflagellate
Dinophyta (Pyrrhophyta)	Dinoflagellates	Chlorophyll *a* Chlorophyll *c*	Mostly marine	Mostly unicells, some coccoids and filaments; biflagellate
Haptophyta		Chlorophyll *a* Chlorophyll *c*	Mostly marine	Unicellular biflagellates
Euglenophyta	Euglenoids	Chlorophyll *a* Chlorophyll *b*	Mostly freshwater	Unicellular uniflagellates
Chlorophyta	Green algae	Chlorophyll *a* Chlorophyll *b*		
Prasinophyceae			Marine and freshwater	Unicells; 1–8 flagella
Chlorophyceae			Mostly freshwater; some terrestrial and marine	Unicellular, coccoid, or colonial flagellates; multicellular or multinucleate filaments; bi- or tetraflagellate
Ulvophyceae			Marine or subaerial	Uni- or multicellular or multinucleate filaments; reproductive cells bi- or tetraflagellate
Pleurastrophyceae			Subaerial	Coccoid or filament; reproductive cells biflagellate
Charophyceae	Stoneworts or brittleworts; desmids		Fresh or brackish water or subaerial	Coccoid or filament, reproductive cells biflagellate or with no flagella; or multinucleate cells, complex thalli with biflagellate male gametes

history of algae, which spans at least five hundred million years, the definition has narrowed considerably. For instance, the assemblage of organisms traditionally called the blue-green algae will not be discussed here. These organisms are now known as **cyanobacteria**, a name that more accurately reflects their nature as **prokaryotes**. The algae are now generally considered to include only **eukaryotic** organisms.

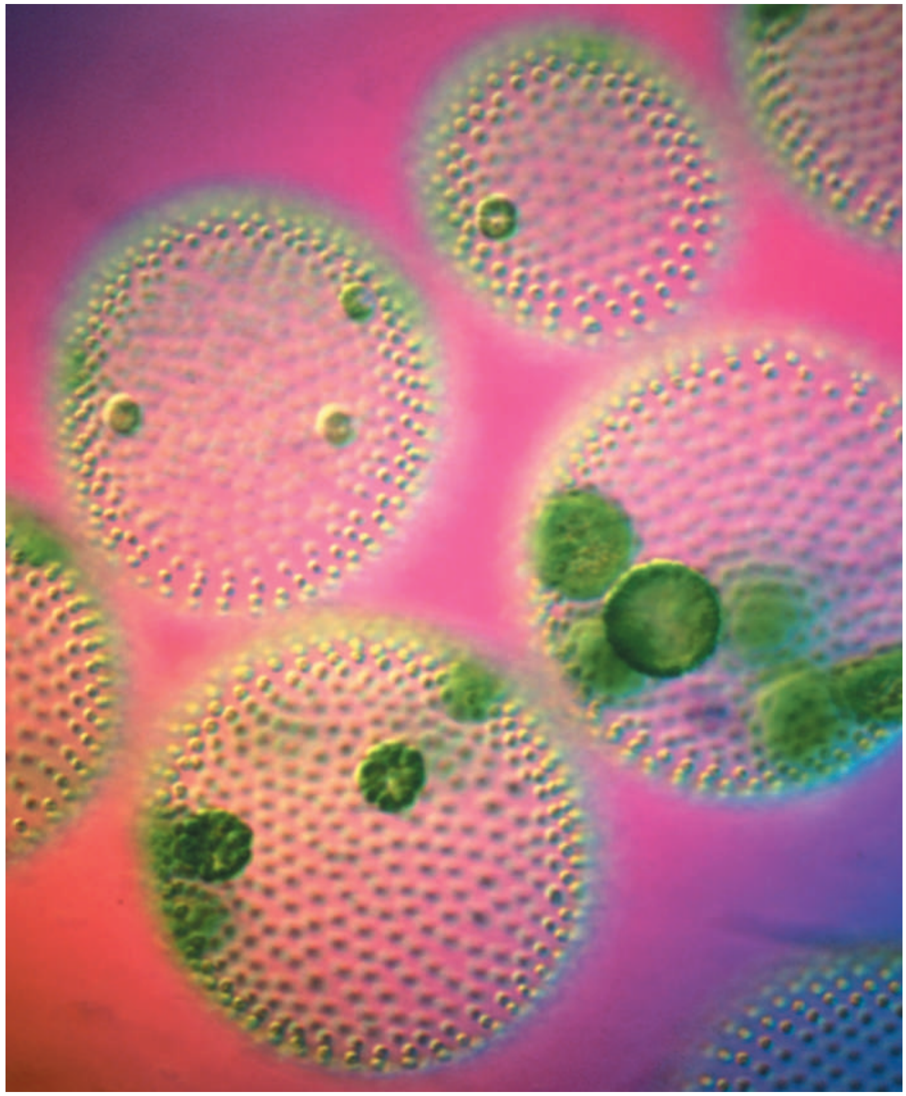
Even after narrowing the group by excluding cyanobacteria, a succinct, precise definition of algae is not really possible. It would be accurate to say that algae are eukaryotic, photosynthetic **autotrophs** (and their colorless relatives), and that most are aquatic (there are some terrestrial species). The

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

eukaryotic a cell with a nucleus

autotrophs "self-feeders"; any organism that uses sunlight or chemical energy



Green algae magnified fifty times their original size.

algae include organisms ranging in size from the microscopic to those reaching lengths as tall as a six-story building (e.g., the giant kelp, *Macrocystis*, which exists off the California coast), but no species of alga achieves the **morphological** complexity of true land plants; furthermore, sexual reproduction in algae is completely different than that of true land plants. Although not as beautiful to most people as roses and redwood trees, the algae are arguably the most important photosynthesizing eukaryotes on Earth.

morphological related to shape

Data analysis based on morphological, biochemical, and molecular research has led many systematists (scientists who study relationships among organisms) to conclude that traditional classification schemes for algae, and plants in general, do not reflect natural groupings and so should be abolished. It is useful, nevertheless, to have a classification system that provides a structure for comparing and discussing the various groups in terms that phycologists (scientists who study algae) and other scientists who work with algae (such as ecologists and biochemists) and students can understand. The accompanying table compares different groups of algae at the taxonomic level of division using a scheme that is generally accepted by many phycologists.

Of the eight divisions of algae in the table, only the group called the Chlorophyta is considered to be closely related to green plants. The organisms in the other groups are considered to be more closely related to **protists** than to green plants.

protist usually a single-celled organism with a cell nucleus, of the kingdom Protista

An ancient unicellular green alga gave rise to all algae in the Chlorophyta **lineage**. Green algae within the Chlorophyta are further split into two groups, one that contains the charophycean algae and another that consists of all other green algae. It is generally accepted among botanists (scientists who study plants) that a charophycean alga is the closest ancestor to the higher green plants.

lineage ancestry; the line of evolutionary descent of an organism

Without the ancestral green algae, there would be no land plants, and without the algae and land plants, life as we know it would not be possible. Algae are primary producers in any aquatic environment. They are the basis of the food web, forming the very bottom of the food chain, meaning that they provide, as a byproduct of photosynthesis, a majority of the oxygen humans and animals breathe.

Some algae form **symbiotic** relationships with other organisms. Specific algae, in association with various types of fungi, form lichens of many different species, one of which is a major food source for reindeer in arctic regions. Algae can also form symbiotic relationships with animals, as evidenced by the very successful association of some reef-forming corals and the dinoflagellate algae of the species *Symbiodinium*.

symbiosis a relationship between two organisms from which each derives benefit

Many algae are of economic importance. The fossilized remains of **diatoms**, known as diatomaceous earth, are used in cleaning products and as filtering and **inert** processing agents. Algal **polysaccharides** provide agar, used to prepare media for culturing bacteria, fungi, and plant tissues and in the purification and separation of nucleic acids and proteins. In Asia, certain algae are a major source of food. A tour through an Asian food store will turn up innumerable products made with algae, including the red alga, *Porphyra* (also known as nori or laver), which is used as a wrapper for sushi; prepared packets of dried soups featuring green algae; and several species of red and brown algae that are packaged, dried, salted, refrigerated, pickled, or frozen. The red alga *Chondrus crispus* provides carrageenan, used in the food industry as a thickener and **emulsifier** in many brands of ice cream, pudding, baby food, and chocolate milk. Brown algae provide alginates, also used as thickeners and stabilizers in numerous industries including food, paints, and cosmetics. Algal seaweeds are also collected and used as fodder for livestock in many parts of the world.

diatoms hard-shelled single-celled marine organisms

inert incapable of reaction

polysaccharide a linked chain of many sugar molecules

emulsifier a chemical used to suspend oils in water

Some algae are of concern to humans because of the problems they cause. Some algae grow on the sides of buildings and on statues or other structures, forming unsightly discoloration. Rarely, and generally only in immuno-compromised individuals, certain species of green algae invade human tissues, initially gaining entry through a cut or abrasion on the skin and then proliferating. The green alga *Cephaleuros virescens* can become parasitic on the leaves of economically important plants such as coffee and tea. But, by far, the most destructive algal incidents are harmful algal blooms (HABs), the consequences of which can cost millions of dollars and cause serious health problems to livestock, fish, and even humans. HABs can occur in freshwater, contaminating watering sources for livestock and killing fish, or in marine environments. The marine HAB known as red tide is caused by

Giant kelp growing in a sheltered bay in the Falkland Islands.

toxin a poisonous substance

certain **toxin**-producing dinoflagellates. The toxin can poison fish and shellfish, and shellfish contaminated by the toxin can cause mild to severe illness, even death, in humans who consume them. The alga *Pfiesteria* has caused toxic reactions in fish and humans in estuaries in the southeastern United States. Many HABs can be attributed to pollution, especially runoff into waterways that causes a nutrient-rich environment conducive to the rapid growth of algae.

Divisions of Algae

chloroplasts the photosynthetic organelles of plants and algae

The type of chlorophyll and other pigments is characteristic of certain groups of algae. For instance, the Chlorophyta (and the pigmented members of the euglenoids) have both chlorophylls *a* and *b*. These pigments are contained in **chloroplasts** that are the result of endosymbiotic events; that is, during the evolutionary history of the algae, photosynthetic, prokaryotic organisms survived being ingested by their algal hosts and became an integral part of them. The main features distinguishing the algal divisions are listed in the accompanying table. Here are a few more details:

Glaucophyta. The glaucophytes are unusual unicells in which the plastids are recent endosymbionts.

Cryptophyta. The cryptomonads are unicells with phycobiliprotein pigments like the red algae, but the pigments are located in a different position within the chloroplast.

Haptophyta. The haptophytes are distinguished by the haptonema, an anterior **filament** that sometimes serves to attach the unicells to a substrate or to catch prey. The haptophytes include the coccolithophorids, the scales of which formed the white cliffs of Dover on the coast of England.

filament a threadlike extension of the cell membrane or other part of an organism

Dinophyta (or Pyrrhophyta). The dinoflagellates provide a good example of the problems in classifying algae, as many species do not have chloroplasts and, thus, live heterotrophically. As discussed above, some species are notorious for causing HABs, including red tides.

Euglenophyta. The euglenoids are **motile** unicells often found in organically enriched waters; like the dinoflagellates, some species of euglenoids are colorless heterotrophs.

motile capable of movement

Heterokontophyta (or Ochrophyta). This large division includes the brown algae (class Phaeophyceae) and the diatoms (Bacillariophyceae). Brown algae are mostly seaweeds, very diverse in form and habitat. They range in size from microscopic filaments to kelps 50 or 60 meters in length. *Sargassum* floats freely in the Sargasso Sea, but some kelp, such as *Laminaria*, have a holdfast that attaches to a substrate, leaving the stem and leafy blade to undulate in the current.

Diatoms are noted for their **siliceous** walls, which can form many intricate and beautiful shapes. Diatoms are very abundant in both freshwater and marine environments and are important primary producers.

siliceous composed of silica, a mineral

Rhodophyta. The red algae are mostly seaweeds, and they form some of the most beautiful, exotic shapes of all algae. Some species are calcified and resemble corals.

Chlorophyta. The very diverse green algae form two major lineages. The charophycean algae have complex morphologies and **ultrastructural** and genetic features that indicate they are ancestral to land plants. The other lineage comprises all other green algae, which range from unicells to large multinucleate filaments. SEE ALSO Aquatic Ecosystems; Cyanobacteria; Endosymbiosis; Evolution of Plants.

ultrastructural the level of structure visible with the electron microscope; very small details of structure

Russell L. Chapman and Debra A. Waters

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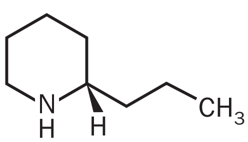
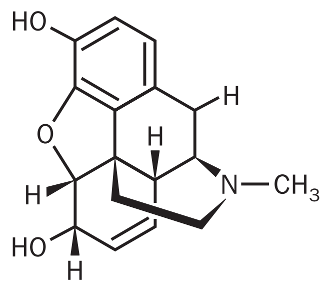
Alkaloids

Alkaloids are natural, organic substances that are predominantly found in plants and normally contain at least one nitrogen atom in their chemical structure. Their basic (alkaline) nature has led to the term *alkaloids.* Since the identification of the first alkaloid, morphine, from the opium poppy (*Papaver somniferum*) in 1806, more than ten thousand alkaloids have been isolated from plants. Alkaloids are the active components of numerous medicinal plants or plant-derived drugs and poisons, and their structural diversity

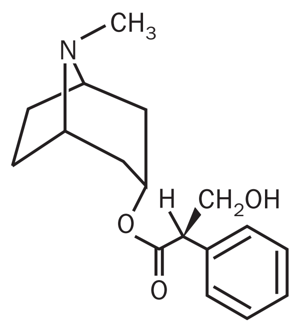
Structures of some alkaloids, with the names of the plants that produce them.



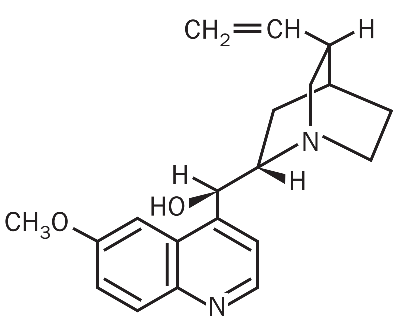
Coniine
Piperidine alkaloid
Conium maculatum



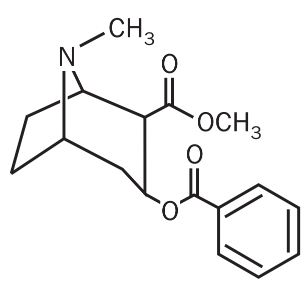
Morphine
Isoquinoline alkaloid
Papaver somniferum



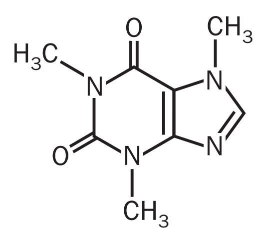
Atropine
Tropan alkaloid
Hyoscyamus niger
Atropa belladonna



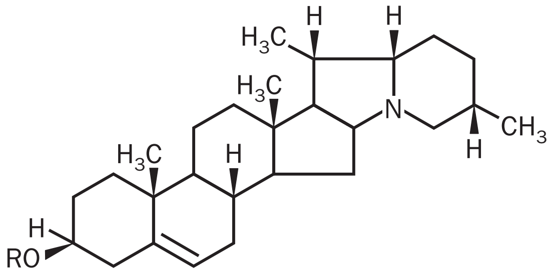
Quinine
Quinoline alkaloid
Cinchona officinalis



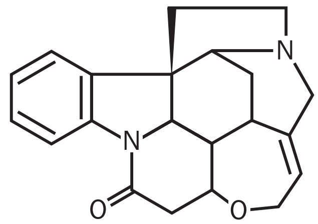
Cocaine
Tropan alkaloid
Erythroxylon coca



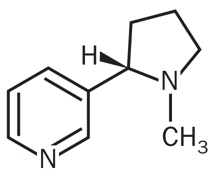
Caffeine
Purine alkaloid
Coffea arabica



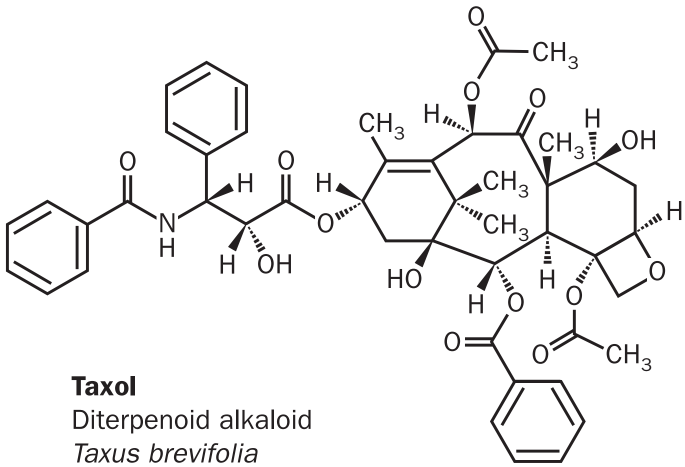
Solanine
Steroid glycoalkaloid, R=solatriose
Solanum tuberosum



Strychnine
Indole alkaloid
Strychnos nux-vomica



Nicotine
Pyridine alkaloid
Nicotiana tabacum



Taxol
Diterpenoid alkaloid
Taxus brevifolia

Structures of some alkaloids, with the names of the plants that produce them.

and different **physiological** activities are unmatched by any other group of natural products.

physiology the biochemical processes carried out by an organism

Although alkaloids have been detected in some animals (e.g., in the toxic secretions of fire ants, ladybugs, and toads), their major occurrence is in the flowering plants. Alkaloids are relatively stable **compounds** that accumulate as end products of different biosynthetic pathways, mostly starting from common amino acids such as lysine, ornithine, tyrosine, tryptophan, and others. Their classification is usually based on the formed **heterocyclic** ring system (e.g., piperidine in coniine, pyridine in nicotine, and quinoline in quinine). Some structures are relatively simple, whereas others are quite complex.

compound a substance formed from two or more elements

heterocyclic a chemical ring structure composed of more than one type of atom, for instance carbon and nitrogen

Alkaloids can occur in all parts of the plant but frequently, depending on the plant species, they accumulate only in particular organs (e.g., in barks, roots, leaves, and fruits), whereas at the same time other organs are alkaloid-free. In potato plants, the edible tubers are devoid of alkaloids, whereas the green parts contain the poisonous solanine. The organ in which alkaloids accumulate is not always the site of their synthesis. In tobacco, nicotine is produced in the roots and translocated to the leaves where it accumulates.

The functions of alkaloids in plants are mostly unknown, and their importance in plant metabolism has been much debated. A single plant species may contain over one hundred different alkaloids, and the concentration can vary from a small fraction to as much as 10 percent of the dry weight. Breeding for plants devoid of alkaloids has also demonstrated that alkaloids are apparently not vital. Why does a plant invest so much nitrogen and energy in synthesizing such a large number and quantity of compounds? Most alkaloids are very toxic and, therefore, have the potential to function in the chemical defense arsenal of plants against attack by **herbivores** and microorganisms. For example, the nicotine present in tobacco leaves inhibits the growth of tobacco hornworm larvae; the purified compound is also applied as an effective insecticide in greenhouses. In addition, alkaloids have been suggested to serve as a storage form of nitrogen or as protectants against damage by ultraviolet light.

herbivore an organism that feeds on plant parts

Alkaloids have traditionally been of great interest to humans because of their pronounced physiological and medicinal properties. From the beginning of civilization, alkaloid-containing plant extracts have been used in all cultures as potions, medicines, and poisons. Greek philosopher Socrates died in 399 B.C.E. by consumption of coniine-containing hemlock (*Conium maculatum*), and Egyptian queen Cleopatra (69–30 B.C.E.) used atropine-containing plant extracts (such as **belladonna**) to dilate her pupils. In modern times, the stimulants caffeine in coffee, tea, and cacao and nicotine in cigarettes are consumed worldwide. Alkaloids with **hallucinogenic**, narcotic, or **analgesic** properties have found medical application as pure compounds (e.g., morphine, atropine, and quinine) or served as model compounds for modern synthetic drugs, while several are abused as illegal drugs (e.g., cocaine). Other alkaloids are too toxic for any therapeutic use (e.g., coniine and strychnine), but plant constituents are still screened for new, biologically active compounds. An example is the discovery of taxol, which has **cytostatic** properties and is applied as an anticancer drug. SEE ALSO Cacao; Coca; Coffee; Defenses, Chemical; Medicinal Plants; Opium Poppy; Poisonous Plants; Potato; Tobacco.

belladonna the source of atropine; means "beautiful woman," and is so named because dilated pupils were thought to enhance a woman's beauty

hallucinogenic capable of inducing hallucinations

analgesic pain-relieving

cytostatic inhibiting cell division

Erich Kombrink

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Allelopathy

Allelopathy describes those situations and events where chemicals produced by higher plants, algae, fungi, or microorganisms cause some effect, either inhibitory or stimulatory, on other members of the plant or microbial **community**. Unlike competition for a resource, the central principle in allelopathy arises from the fact that plants and microorganisms collectively produce thousands of chemicals, and many of these chemicals are released from the producing organism by leaching, **exudation**, **volatilization**, or decomposition processes. Subsequently, some of these **compounds** (known as allelochemicals) alter the growth or **physiological** functions of organisms that encounter them during growth. For example, almost pure droplets of sorgoleone (a quinone) are exuded from the roots of *Sorghum* species, and sorgoleone inhibits growth in plants that contact it by blocking photosynthesis and respiration. While the word "allelopathy" was first used in the 1930s, the phenomenon that it describes was suggested by natural philosophers more than two thousand years ago as they observed that some plants did not grow well near other kinds of plants.

community a group of organisms of different species living in a region

exudation releasing of a liquid substance; oozing

volatilization release of a gaseous substance

compound a substance formed from two or more elements

physiology the biochemical processes carried out by an organism

Research conducted in the last half of the twentieth century demonstrated cases of growth inhibition by allelochemicals that influenced vegetational patterns, rate and sequences in plant succession, weed abundance, crop productivity, and problems in replanting fruit and other crops. Investigators have focused on identifying the producing plants and the chemicals they give off, the physiological effects on receiving species, and how climatic and soil conditions change the action of allelochemicals. Cinnamic and benzoic acids, **flavonoids**, and various terpenes are the most commonly found allelochemicals, but several hundred chemicals have been identified, including many other classes of secondary plant compounds. A few allelochemicals have been developed as herbicides and pesticides, and it may be possible to genetically engineer a crop to produce its own herbicides. SEE ALSO Flavonoids; Interactions, Plant-Plant.

flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

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Alliaceae

The Alliaceae or onion family was once included in the monocot family Liliaceae, but is now recognized by many as a separate plant family. The family includes herbaceous (nonwoody) monocot plants that are generally perennial but not evergreen. Most are native to dry or moderately moist regions and other open areas. The family includes bulb or corm-forming plants as well as plants without bulbs or corms. Leaves may be round, flat, or angular in cross section and are alternately or spirally arranged. The leaves of most species in the Alliaceae are aromatic, frequently smelling like onion.

Flowers are generally organized into ball- or umbrella-shaped clusters called umbels.

genera plural of genus

Alliaceae includes several **genera**. Most genera are not commonly grown, although some species, including examples from *Tulbaghia*, *Nothoscordum*, and *Ipheion*, are occasionally grown as ornamentals. The only widely grown genus in the family is *Allium*, with approximately five hundred species that are native throughout the Northern Hemisphere. Important *Allium* species used for food include onion and shallot (*A. cepa*), garlic (*A. sativum*), leek and elephant garlic (*A. ampeloprasum*), Japanese bunching onion (*A. fistulosum*), chives (*A. schoenoprasum*), and garlic chives (*A. tuberosum*).

Many *Allium* species are also grown as ornamentals including *A. giganteum*, *A. christophii*, *A. karataviense*, *A. aflatunense*, *A. caeruleum*, the nodding onion (*A. cernuum*), the yellow-flowered *A. moly*, and the interspecific cultivar Globemaster. A few *Allium* species are also noxious weeds in some parts of the world (e.g., *A. vineale* and *A. triquetrum*). The consumption of garlic has been shown to significantly reduce both blood levels of cholesterol and the chance of coronary heart disease. Evidence also suggests that garlic has anticancer and antibiotic properties and can reduce hypertension and blood clotting. Other alliums, particularly onion, have some of the same health benefits of garlic, but effects vary widely between species. SEE ALSO Economic Importance of Plants; Monocots.

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Anatomy of Plants

The anatomy of plants relates to the internal structure and organization of the mature plant body, especially the vegetative organs of plants.

protoplast the portion of the cell within the cell wall

vesicle a membrane-bound cell structure with specialized contents

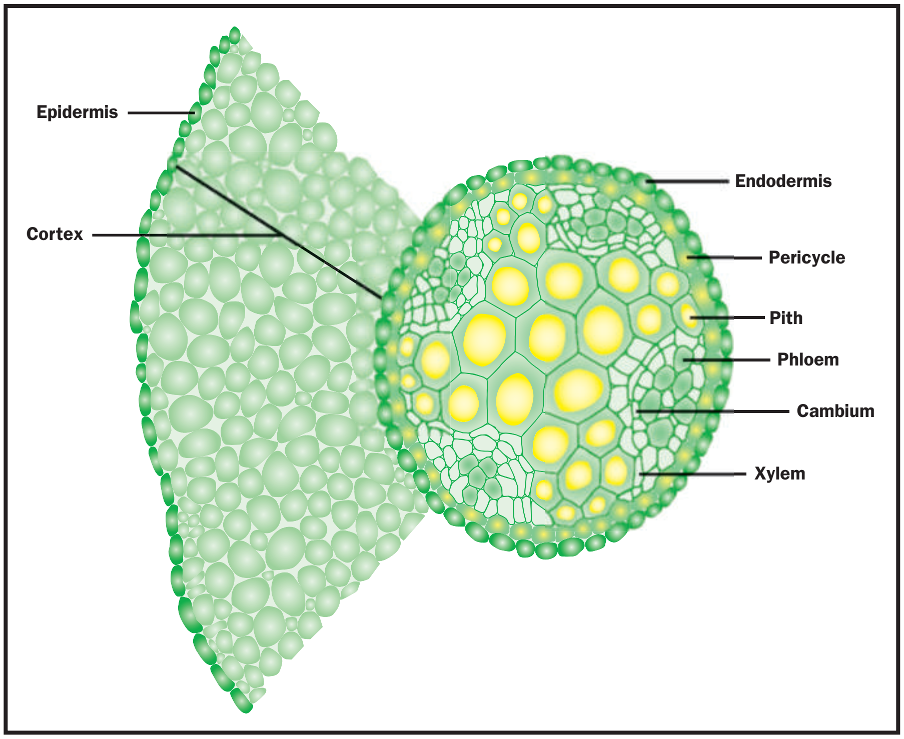
dictyosome any one of membranous or vesicular structures making up the Golgi apparatus

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Use for storage and maintaining internal pressure

lignified composed of lignin, a tough and resistant plant compound

Cells

As in all other organisms, cells make up the fundamental unit of the plant body. Plant cells, whether formed in vegetative or reproductive organs, are usually bounded by a thin, mostly cellulosic wall that encloses the living **protoplast**. Young cells characteristically develop numerous membrane-bound **vesicles**, originating from the endoplasmic reticulum (ER) and **dictyosomes**. Some of these immature cells retain their ability to divide and are called meristematic. As cells age, the vesicles grow together, usually forming one relatively large water-filled **vacuole** positioned in the cell's center, which inhibits further cell division. Some older cells additionally produce a thick **lignified** cell wall located between the cellulosic wall and the protoplast. Cell walls are ordinarily considered a part of the cell's nonliving environment, but considerable research has revealed that a number of important physical and chemical events take place within cell walls.



Transverse section of tissues of a dicot root. Redrawn from Van de Graaff et al., 1994.

Tissues

Groups of adjacent cells having similar structure and function constitute the tissues of the plant. Tissues having a structural or functional similarity comprise the plant organs. All of the cells, tissues, and organs trace their origins back to the **zygote** or embryo, which develops within the seed. Meristematic tissues within the embryo and young plant are responsible for generating new cells that ultimately result in increased plant size. **Apical** meristems develop near the ends of all stems and roots, and they contribute to the increased length of both. **Lateral** meristems (cambia), such as the **vascular** cambium and cork cambium are responsible for increased diameter, especially noticeable in long-lived tree species. The vascular cambium is initiated more internally within the plant body, producing cells both interiorly and exteriorly. Xylem tissue is produced interiorly and phloem tissue is produced exteriorly. The thick-walled secondary xylem tissue constitutes the wood, while all tissues outside of the vascular cambium, including the cork cambium, comprise the plant's bark. Tissues produced by the apical meristems result in the primary growth of the plant, while tissues resulting from cell divisions of the cambia result in secondary growth.

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

apical at the tip

lateral away from the center

vascular related to transport of nutrients

One way in which plant tissues are categorized is on the basis of their cell wall thickness. Parenchyma tissue is composed of evenly thin-walled cells, having cellulosic walls. Sclerenchyma tissue is composed of evenly thick-walled cells as a result of developing both cellulosic and lignified wall layers. Collenchyma tissue is an intermediate tissue type having unevenly thickened cells aggregated together. Sclerenchyma tissue functions both in support and water conduction, while parenchyma participates in food storage, cell division, and food conduction. Collenchyma is the least common tissue type among the three and may be involved in a combination of activities associated with the other two types.

Plant tissues can also be characterized by their relative position within the plant organs. There are three tissue systems within the mature plant: the dermal, the vascular, and the ground tissue systems. Dermal tissues compose the outermost tissue layer, the epidermis. Xylem and phloem are prominent tissues comprising the vascular system of the plant. In the root, the vascular system (also referred to as the vascular cylinder or stele) has as its outer boundary a single layer of pericycle tissue that is immediately exterior to the xylem and phloem. The pith, composed of thin-walled cells, may develop immediately interior to the vascular tissues, more centrally located in stems and roots. Root pericycle is a common tissue of origin for the formation of lateral roots, while the pith tissue is involved in food storage. Positioned in between the dermal and vascular tissue systems is the ground system, often referred to as the cortex. The cortex of younger stems and roots may be further partitioned from outside to inside into the hypodermis, the **cortical** parenchyma, and the endodermis. The endodermis of underground roots and stems, especially, often develops waxy deposits of suberin in the cell walls. These water-impervious deposits are referred to as Casparian thickenings and are believed to prevent the diffusion of water and dissolved substances along the cell walls, directing the movement through the protoplast.

cortical relating to the cortex of a plant

The dermal and ground tissue systems of roots and stems of older tree species may be sloughed off by the activity of the ever-increasing circumference of the vascular cambium. In these older organs another dermal tissue, the cork, is produced outwardly by the cork cambium. The enclosing cork functions not only as a protective surface layer but also as a tissue involved in water conservation.

Organs

Organs of the plant body can be classified as either vegetative or reproductive. Usually the vegetative organs are involved in procuring required nutrients for the plant. For example, the green photosynthetic leaves are responsible for the production of food, while the roots can function as excellent food storage organs, as well as obtaining water and dissolved minerals by absorption from the soil. Cellular extensions of the root epidermal cells, the root hairs, increase the absorbing surface of roots. Stem organs, developing between the leaves and the roots, produce conducting tissues (xylem and phloem) responsible for transporting food, water, and dissolved substances throughout the rest of the plant. Reproductive organs of the **angiosperms** are the flowers, fruits, and seeds. These three organs are ordinarily involved in sexual reproduction, while the vegetative organs may function in asexual reproduction.

angiosperm a flowering plant

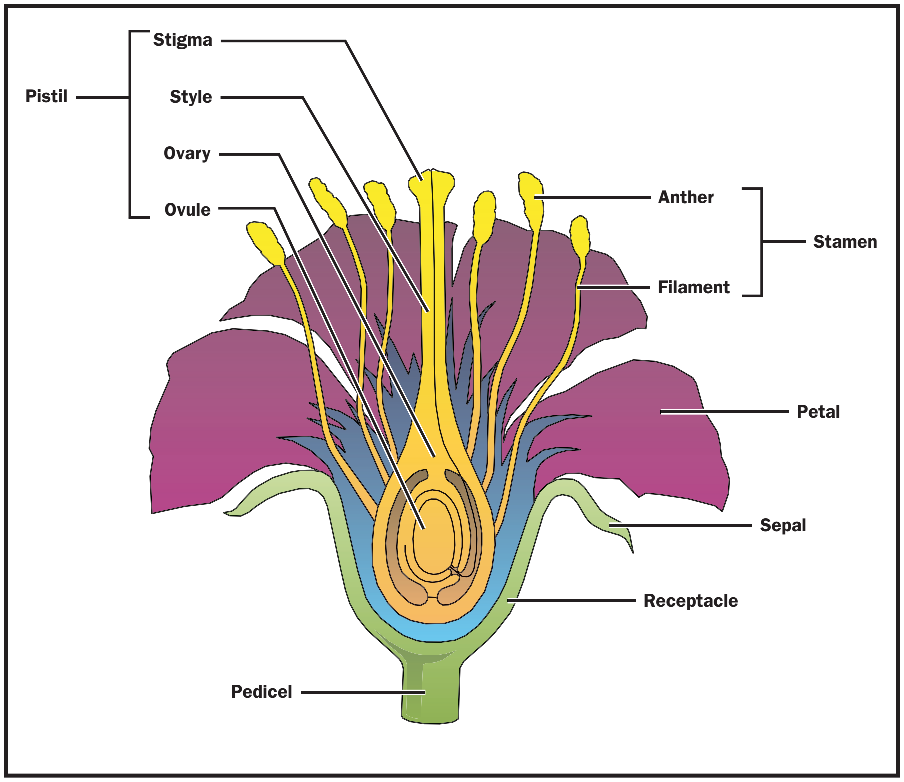
appendages parts that are attached to a central stalk or axis

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

whorl a ring

Complete flowers are composed of the four **appendages** produced by the reproductive apical meristem of the stem: **sepals**, petals, stamens, and **carpels**. The **whorl** of petals can be quite conspicuous, attracting pollinators such as insects to the flower, where pollen can be inadvertently gathered from the stamens. The carpels together constitute the pistil, the component parts of which are the landing pad for the pollen (the stigma), the style, and the basal ovary. Ovules develop within the ovary, and following fertilization give rise to the seeds and fruit, respectively.



Structure of angiosperm flowers. Redrawn from Van de Graaff et al., 1994.

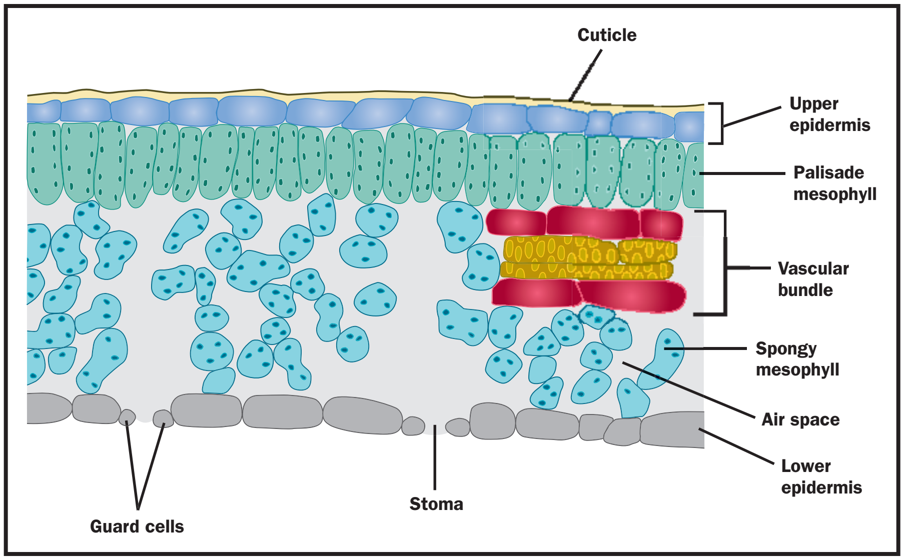
Organs of the embryo or young plant are used to distinguish the two large groups of flowering plants. The monocotyledonous and dicotyledonous plant groups produce one or two embryonic cotyledons, respectively. Both internal and external features of both vegetative and reproductive organs can be used to distinguish the monocots from the dicots. The more prominent leaf veins have venation patterns that are referred to as reticulate (netlike) in the dicots and parallel venation in monocots. The number of floral appendages (sepals, petals, stamens, and carpels) can also be used to identify the two angiosperm groups. Dicot species usually produce the separate floral appendages in whorls of fours or fives, while the monocots develop whorls of appendages in threes. Whole number multiples of these base numbers can similarly be used to distinguish the two groups.

Leaves

Leaves, produced as appendages or outgrowths from the vegetative stem apical meristem, have a different tissue arrangement than the stems and roots. The component tissues of the leaf are the epidermis, the mesophyll, and the vascular bundles. The epidermis is formed from the surface cell layer of the stem apical meristem. The epidermis serves a protective function.

Vascular bundles, also called veins, are cylindrical traces of xylem and phloem that diverge from the stem's central stele. The leaf's midvein is the largest medianly positioned vascular bundle. Minor leaf veins develop laterally on either side of the midvein. Both the midvein and minor veins differentiate through the stalk of the leaf (the petiole) into its flat blade.

Transverse section of a dicot leaf. Redrawn from Van de Graaff et al., 1994.



The blade is composed mostly of mesophyll tissue that develops interior to the enveloping leaf epidermis and surrounds the vascular bundles. Most leaves have two types of mesophyll cells, the palisade and spongy mesophyll. Palisade mesophyll develops near the upper epidermis and is composed of columnar-shaped cells. The spongy mesophyll cells are more spherically shaped and are characterized by the presence of numerous intercellular spaces between adjacent cells. Plants produce most of their food during photosynthesis in cells of the mesophyll tissue.

compound a substance formed from two or more elements

organelle a membrane-bound structure within a cell

chloroplast the photosynthetic organelle of plants and algae

Although considerable variation in anatomy occurs in the internal leaf tissues of dicots and monocots, the differences are mostly based on environmental rather than taxonomic criteria. There is a distinct difference, however, in the leaf anatomy of certain species, both dicot and monocot, based on whether the first product produced in photosynthesis is a three-carbon or a four-carbon (C_4) **compound**. C_4 plants, best represented by tropical grasses, develop a thick-walled cell layer around each leaf vascular bundle, called the bundle sheath cells. This concentric organization of surrounding bundle sheath cells is referred to as Kranz (German for "wreath") anatomy. Additionally, the bundle sheath cells contain more **organelles** such as mitochondria and **chloroplasts**. Dicot and monocot species in which the first photosynthetic compound produced is a three-carbon compound do not exhibit Kranz anatomy.

Stems and Roots

The arrangement of the vascular tissues within the stele not only distinguishes dicot from monocot species, but also provides a means of identifying the specific vegetative organs. Stems are partitioned into nodes and internodes. Nodes are the locations of leaf development, while the internodes are the distances between the leaves, comprising most of the stem's length. Young dicot internodes usually develop a single ring of vascular bundles when viewed in cross sections. As a result of vascular cambium activity in older woody dicots, the vascular bundles are disrupted and eventually give way to concentric rings of secondary xylem interiorly and secondary phloem exteriorly. The major secondary phloem cell type involved in food conduction is the sieve-tube element. The interiorly produced secondary xylem is composed of **tracheids** and vessel elements, the water-conducting cells, which have heavily lignified cell walls. The majority of dicot tree species are composed of these thick-walled xylem cells, which represent the wood or lumber used in commerce. A central pith, with peripheral **vascular** tissues, develops in the center of both dicot and monocot stems, as well as monocot roots. The stems of many monocot species (for example, grain crops) produce a scattered arrangement of vascular bundles that develop throughout the pith and cortex. These vascular bundles do not become disrupted in older stems, since no vascular cambium develops in monocot species. Thus, young and old monocot stems resemble each other in their anatomy. Young and old dicot roots do not develop a central pith but have xylem in their centers. Vascular bundles, so characteristic of stems and leaves, are absent throughout most of the length of roots in both angiosperm groups.

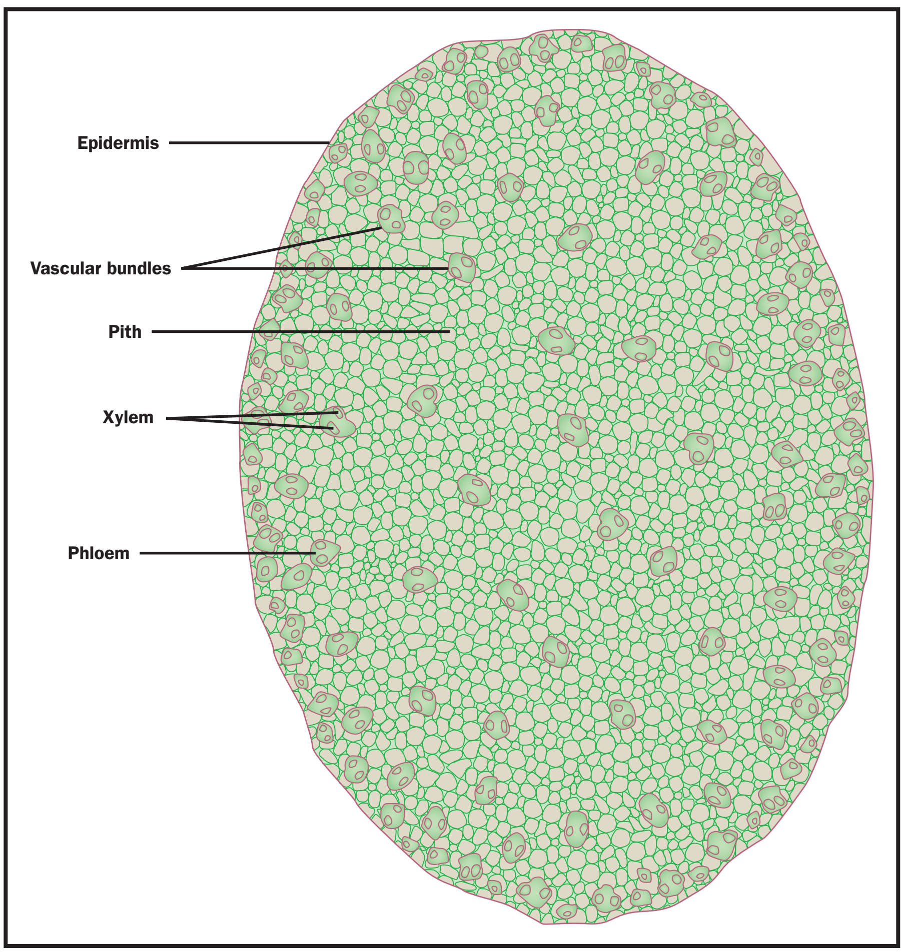
tracheid a type of cell that conducts water from root to shoot

vascular related to transport of nutrients

The stems and roots of flowering plants are categorized by their appearance. For example, stem structural types include bulbs, rhizomes, corms, tubers, and **stolons** that develop underground. **Cladodes**, tendrils, tillers,

stolons an underground stem that may form new individuals by sprouting

cladode a modified stem having the appearance and function of a leaf



Transverse section of a monocot (*Zea mays;* corn) stem. Redrawn from Van de Graaff et al., 1994.

and thorns are types of aboveground stems. Root structural types include underground tap and fibrous roots, while buttress and prop roots occur above ground.

Bryophytes and Ferns

Two important groups of nonflowering plants include the bryophytes and the ferns. The bryophytes include the mosses, liverworts, and hornworts. They lack vascular tissues, and therefore do not develop true leaves, stems, and roots. Since bryophytes produce organs that are similar in structure and function to leaves and stems, these organ names are used, however. Being nonvascular plants, bryophytes ordinarily form a low-growing ground cover, never becoming a conspicuous part of the temperate vegetation. While most cells are thin-walled and spherical, elongated cells of conducting tissues develop within the stems of some bryophytes. Leptome and hydrome are analogous to the phloem and xylem tissues of higher plants, respectively. Leaves of bryophytes are produced spirally around the stem. Leaves contain **filaments** of cells, the photosynthetic **lamellae**.

filament a threadlike extension

lamellae thin layers or plate-like structures

Ferns are primitive vascular plants and commonly have complicated arrangements of phloem and xylem tissues within stem and root steles. Most temperate ferns develop elongated underground stems (rhizomes) from which the aboveground leaves (fronds) originate. Developing on the lower side of the rhizome are the slender roots. Fronds, on their inception, are tightly coiled into fiddleheads, termed such because of their resemblance to the carvings on the end of a violin or fiddle. One of the most conspicuous attributes of ferns is the formation of older leaves that are compound, giving them a dissected or lacy appearance. Reproductive structures commonly develop on the underside of fern fronds and are conspicuous due to their brown color in contrast to the leaf's green background. These are the sori in which spores are produced. No development of flowers, fruits, or seeds occurs in the ferns. SEE ALSO BARK; BRYOPHYTES; CELLS; CELLS, SPECIALIZED TYPES; FERNS; FLOWERS; LEAVES; MERISTEMS; ROOTS; STEMS; TISSUES.

Jan E. Mikesell

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Angiosperms

The angiosperms, or flowering plants (division Anthophyta or Magnoliophyta), comprise more than 230,000 species and are thus by far the largest division of plants; they represent the dominant group of land plants today. In both vegetative and floral **morphology** the angiosperms are highly diverse. In size, for example, they range from the duckweeds (the genus *Lemna*), which are roughly one millimeter in length, to *Eucalyptus* trees, which are well over one hundred meters. Although all are characterized by the possession of flowers, these structures are also highly diverse in form and size. The smallest flowers are less than a millimeter in size (the flowers of duckweeds) while the largest flowers are approximately one meter in diameter (the flowers of *Rafflesia*). Features unique, or nearly so, to angiosperms include the flower; the presence of seeds within a closed structure (actually a modified leaf) referred to as the **carpel**; the reduction of the female **gametophyte** to eight nuclei and seven cells; double fertilization (the

morphology shape and form

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

gametophyte the haploid organism in the life cycle

MAJOR ANGIOSPERM GROUPS

Major Clades and Representative Families	Common Name	Number of Species in Family (approximate)
Eurosid		
Rosaceae	Rose family	3,500
Fabaceae	Pea or legume family	17,000
Brassicaceae	Mustard family	3,000
Fagaceae	Beech or oak family	1,000
Cucurbitaceae	Pumpkin or gourd family	700
Euphorbiaceae	Spurge family	5,000
Juglandaceae	Walnut or hickory family	50
Begoniacae	Begonia family	1,000
Geraniaceae	Geranium family	750
Malvaceae	Cotton family	1,000
Euasterid		
Cornaceae	Dogwood family	100
Ericaceae	Heath family	3,000
Lamiaceae	Mint family	3,000
Solanaceae	Tomato or potato family	2,500
Asteraceae	Sunflower family	25,000
Apiaceae	Parsley family	3,000
Hydrangeaceae	Hydrangea family	170
Caryophyllales		
Cactaceae	Cactus family	2,000
Caryophyllaceae	Carnation or pink family	2,000
Aizoaceae	Mesembryanthemum family	2,300
Portulacaceae	Portulaca family	500
Polygonaceae	Buckwheat or rhubarb family	750
Magnoliids*		
Magnoliaceae	Magnolia family	200
Lauraceae	Avocado or cinnamon family	2,500
Piperaceae	Pepper family	3,000
Myristicaceae	Nutmeg family	380
Annonaceae	Sweetsop family	2,000
Monocots*		
Orchidaceae	Orchid family	18,000
Poaceae	Grass family	9,000
Arecaceae	Palm family	2,800
Araceae	Arum family	2,000

* Indicates major clades that are noneudicots; other major clades are eudicots.

A magnolia in bloom. Magnolias are basal angiosperms (plants thought to have evolved first) and are ancestors to both monocots and eudicots.

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

fusion of egg and sperm resulting in a **zygote** and the simultaneous fusion of the second sperm with the two polar nuclei, resulting in a triploid nucleus) and subsequent **endosperm** formation; a male or microgametophyte composed of three nuclei; stamens with two pairs of pollen sacs; and sieve tube elements and companion cells in the phloem. Nearly all angiosperms also possess vessel elements in the xylem, but vessel elements also occur in Gnetales and some ferns.

Origins of Angiosperms

Because of the sudden appearance of a diverse array of early angiosperms in the fossil record, Charles Darwin referred to the origin of the flowering plants as "an abominable mystery." Although there are reports of earlier angiosperm remains, the oldest fossils that are indisputably angiosperms are from the early Cretaceous period, about 130 million years ago. Based on fossil evidence, it is clear that angiosperms radiated rapidly after their origin, with great diversity already apparent 115 million years ago. By 90 to 100 million years ago the angiosperms had already become the dominant **floristic** element on Earth. By 75 million years ago, many modern orders and families were present.

floristic related to plants

The closest relatives and ancestor of the flowering plants have long been topics of great interest and debate. There was widespread belief during the last decades of the twentieth century that the Gnetales, a group of **gymnosperms** having three existing, highly divergent members (*Gnetum*, *Ephedra*, *Welwitschia*), were the closest living relatives of the flowering plants among existing gymnosperms. These three **genera** resemble angiosperms in having special water-conducting vessels in the wood and reproductive structures organized into compound **strobili** similar in organization to compound flower clusters. In addition, some Gnetales (the genus *Gnetum*) have angiosperm-like leaves. Gnetales also have a process that, in part, resembles double fertilization, a feature unique to angiosperms. In Gnetales, both sperm produced by the male gametophyte (in the pollen) fuse with nuclei in the female gametophyte. However, in Gnetales the second fusion pro-

gymnosperm a major group of plants that includes the conifers

genera plural of genus

strobili cone-like reproductive structures duces an additional embryo and does not result in the triploid endosperm characteristic of flowering plants. Beginning in the mid-1980s, however, **phylogenetic** trees derived from gene sequence data have indicated instead a close relationship of Gnetales to conifers, with all of the living gymnosperms forming a **clade** that is the sister group to the angiosperms. The molecular evidence is compelling and indicates that Gnetales are probably not the closest living relatives of the flowering plants. Several fossil **lineages** have been suggested as close relatives of the angiosperms. These include *Pentoxylon* and Bennettitales, and these plants must be considered as possible candidates for the closest relatives of the flowering plants.

phylogenetic related to phylogeny, the evolutionary development of a species

clade group of organisms composed of an ancestor and all of its descendants

lineage ancestry; the line of evolutionary descent of an organism

Taxonomy

Traditionally, angiosperms have been divided into two major groups or classes: dicotyledons (Magnoliopsida) and monocotyledons (Liliopsida). In recent classification schemes, each class was then divided into a number of subclasses. In this scheme, dicots were divided into six subclasses: Magnoliidae, Hamamelidae, Caryophyllidae, Rosidae, Dilleniidae, and Asteridae. The monocots were similarly divided into subclasses: Alismatidae, Arecidae, Commelinidae, Zingiberidae, and Liliidae. Although the division of angiosperms into monocots and dicots, with subsequent division into subclasses, has long been followed in classifications and textbooks, phylogenetic studies have dramatically revised views of angiosperm relationships. In fact, trees derived from deoxyribonucleic acid (DNA) sequence data have stimulated the most dramatic changes in views of angiosperm relationships during the past 150 years. As reviewed next, DNA data indicate that many of these groups do not hold together (that is, they do not form distinct clades—they are not monophyletic); hence they should not be recognized.

Until recently, the radiation of the angiosperms was thought to have occurred so rapidly that many scientists believed that it might not be possible to identify the earliest angiosperms (this is also known as Darwin's "abominable mystery"). However, a series of recent molecular systematic (DNA) studies using different genes and molecular approaches all identify the very same first branches of the angiosperm tree of life. The evidence from these studies indicates that the angiosperms, formerly grouped as dicots and monocots, are best classified as either eudicots (true dicots) or noneudicots. The noneudicots are further divided into the monocots and the basal angiosperms. This scheme reflects what is now known about angiosperm evolution: The basal angiosperms are those plants thought to have evolved first and are ancestral to both monocots and eudicots. This group is represented by the Magnoliaceae (Magnolia family), Lauraceae (Laurel family), Nymphaeaceae (water lily family), Amborella (a shrub **endemic** to New Caledonia), and a group of shrubs that include *Illicium*, *Schisandra*, *Trimenia*, and *Austrobaileya*. Many of these early diverging angiosperms possess pollen with a single groove, or aperture (line of weakness).

endemic belonging or native to a particular area or country

The monocots, which also have pollen with a single aperture, are believed to have arisen as one line of this earliest group of plants, probably more than 120 million years ago. Eudicots have pollen with three apertures. The details of their origins from basal angiosperms is less clear, but they are believed to have split off perhaps 127 million years ago.

The term *dicot*, therefore, refers to plants that include both the eudicots and the basal angiosperms. Since the basal angiosperms are ancestral to the monocots as well, *dicot* cannot be meaningfully contrasted to *monocot*, and is thus not considered to be a taxonomically useful label.

Whereas *monocot* remains a useful term, *dicot* does not represent a natural group of flowering plants and should be abandoned. That there is no monocot-versus-dicot split in the angiosperms is not a total surprise—botanists have long theorized that the monocots were derived from an ancient group of dicots during the early diversification of the angiosperms, and recent phylogenetic analyses simply confirm this hypothesis.

compound a substance formed from two or more elements

The early branching angiosperms (or noneudicots) comprise not only the monocots, but many of those families (fewer than twenty-five) traditionally placed in the subclass Magnoliidae. Many of these families of early branching flowering plants possess oil cells that produce highly volatile oils referred to as ethereal oils. These ethereal oils are the basis of the characteristic fragrance of these plants; these **compounds** are responsible for the characteristic aroma of many spices, including sassafras, cinnamon, laurel or bay leaves, nutmeg, star anise, and black pepper. The noneudicots are also highly diverse in floral morphology. Familiar families of noneudicot or early diverging angiosperms include woody families such as the magnolia family (Magnoliaceae), the laurel or cinnamon family (Lauraceae), the nutmeg family (Myristicaceae), and the sweetsop or custard-apple family (Annonaceae). Members of these families often have relatively large flowers with numerous parts that may be spirally arranged. Other early branching angiosperms include plants often referred to as paleoherbs. As the name implies, paleoherbs are predominantly herbaceous and have small flowers with very few flower parts. The paleoherbs include the black pepper family (Piperaceae) and wild-ginger family (Aristolochiaceae).

circumscription the definition of the boundaries surrounding an object or an idea

taxa a type of organism, or a level of classification of organisms

Once the noneudicots are excluded, the remaining dicots form a well-supported clade referred to as the *eudicots.* This group contains, by far, the vast majority of angiosperm species; approximately 75 percent of all angiosperms are eudicots. Eudicots include most familiar angiosperm families. Recent phylogenetic trees demonstrate that the eudicots comprise a number of well-supported lineages that differ from traditional **circumscriptions**. The earliest branches of eudicots are members of the order Ranunculales, which include the Ranunculaceae (buttercup family), Papaveraceae (poppy family), Proteaceae (protea family), and Platanaceae (sycamore family). Following these early branching **taxa**, most remaining eudicots form a large clade (referred to as the core eudicots), comprised of three main branches and several smaller ones. The main branches of core eudicots are:

- eurosids, or true rosids (made up of members of the traditional subclasses Rosidae, Dilleniidae, and Hamamelidae)
- the euasterids, or true asterids (containing members of the traditional subclasses Asteridae, Dilleniidae, and Rosidae)
- the Caryophyllales (the traditional subclass Caryophyllidae, plus some Dilleniidae).

Importantly, there is no clade that corresponds to the traditionally recognized subclasses Dilleniidae and Hamamelidae. As noted, these subclasses have members scattered throughout the eudciots—hence, they are not *natural*, or monophyletic groups. Because of the enormous insights that DNA-based studies have provided into relationships within the angiosperms, the use of long-recognized subclass names and group delineations, such as Magnoliidae, Rosidae, Asteridae, Dilleniidae, has been abandoned in recent classification schemes.

Evolution and Adapations

Based on the earliest branches of the angiosperm tree reconstructed from DNA sequence data, as well as fossil evidence, early angiosperms were likely woody shrubs with a moderate-sized flower possessing a moderate number of spirally arranged flower parts. There was no differentiation between **sepals** and petals (that is, **tepals** were present). The stamens did not exhibit well-differentiated anther and **filament** regions (these are often referred to as laminar stamens). The **carpels**, the structures that enclose the seeds, were folded and sealed by a sticky secretion rather than being fused shut, as is the typical condition in later-flowering plants. In contrast, later angiosperms (the eudicots, for example) have well-differentiated sepals and petals and flower parts in distinct **whorls**. Their stamens are well-differentiated into anther and filament regions and the carpels are fused during development.

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

tepal an undifferentiated sepal or petal

filament a threadlike extension of the cell membrane or other part of an organism

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

whorl a ring

By eighty to ninety million years ago the angiosperms were dominant floristic elements. Obvious reasons for their success include the evolution of more efficient means of pollination (the flower for the attraction of pollinators) and seed dispersal (via the mature carpel, or fruit). One important innovation was the evolution of the bisexual flower; that is, the presence of both carpels and stamens in one flower. In contrast, gymnosperms have separate male and female reproductive structures or cones. Bisexual structures may have an advantage over unisexual structures in that the pollinator can both deliver and pick up pollen at each visit to a flower. Other possible reasons for the success of flowering plants involve morphological, chemical, and anatomical attributes. These include the presence in angiosperms of more efficient means of water and carbohydrate (sugar) conduction via vessel elements and sieve tube elements/companion cells, respectively. These anatomical features may be viewed as adaptations for drought resistance. Vessel elements are found in only a few groups other than flowering plants, and the presence of the sieve tube/companion cell pair is unique to the flowering plants.

The evolution of the deciduous habit was also important in the success of the flowering plants. This feature permitted woody plants to lose their leaves and to become inactive physiologically during periods of drought and cold. Other important evolutionary innovations in angiosperms that also may have contributed to their success include a more efficient source of nutrition for the developing embryo through the production of triploid endosperm (in other seed plants the **haploid** female gametophyte tissue nourishes the young embryo) and the protection of ovules and developing seeds inside a novel, closed structure, the carpel. Compared to other plants, the angiosperms also possess enormous biochemical diversity, which includes a diverse array of chemicals that presumably act in defense against **herbivores** and **pathogens**.

haploid having one set of chromosomes, versus having two (diploid)

herbivore an organism that feeds on plant parts

pathogen disease-causing organism

The first seed-producing plants (various lineages of gymnosperms) were wind-pollinated. The angiosperms, in contrast, as well as some gymnosperms (cycads and Gnetales), typically employ a more efficient system—insects feeding on pollen or nectar transfer pollen from one plant to the next. The more attractive the flower of the plant is to the insect, the more frequently the flowers will be visited and the more seed produced. The first angiosperms likely were pollinated by beetles that foraged on pollen and in so doing moved pollen from one flower to the next. Plants with flowers that provided special sources of food for pollinators, such as nectar, had a selective advantage. In this general way angiosperms and insects coevolved, or diversified. The rise and diversification of the diverse array of flower visitors we see today, such as bees, moths, and butterflies, occurred in concert with the increasing diversification of flowers. Both pollinators and angiosperms were influenced by the diversification of the other. SEE ALSO Dicots; Evolution of Plants; Flowers; Gymnosperms; Monocots; Phylogeny; Systematics, Plant; Taxonomy.

Doug Soltis and Pam Soltis

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Anthocyanins

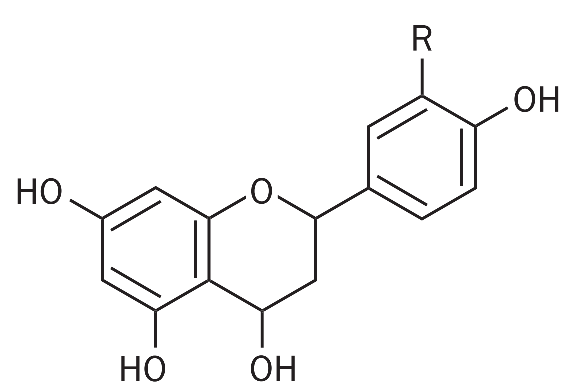
Anthocyanins are a class of molecules pervasive in plants that are responsible for the showy bright purple, red, and blue colors of flowers and variegated leaves. Anthocyanins are located in the **vacuoles** of cells, and different genes control the particular shades of colors. Aside from their coloration, anthocyanin molecules are also active in plant defense mechanisms against insect and fungal attacks and in the recognition of nitrogen-fixing bacteria by leguminous plants (providing a molecule that attracts the bacteria). Approximately twenty genes are involved in the formation of the anthocyanin molecule with various **amendments**, such as **hydroxyl** groups or glucose alterations, to vary the coloration and cause the molecule to function in a particular way. In maize, there are two major types of genes, regulatory and structural,

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Used for storage and maintaining internal pressure

amendment additive

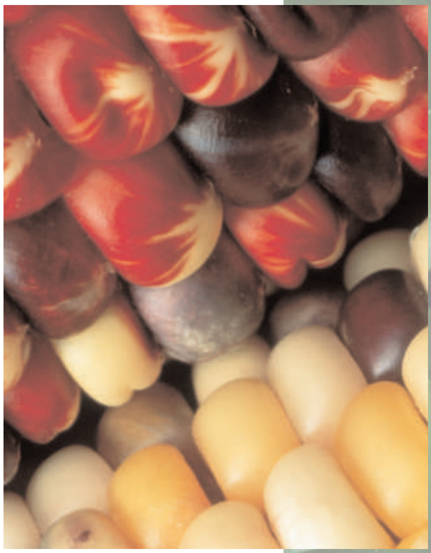
hydroxyl the chemical group -OH

Structure of anthocyanin.



that control the formation of the anthocyanin molecule used to give the corn kernel its color. The variegated Indian corn is caused by an interruption of the color formation by an insert in one of these genes, thus releasing the gene to form color. SEE ALSO FLAVONOIDS; NITROGEN FIXATION; PIGMENTS.

Peter A. Peterson



Variegated Indian corn, whose color is controlled by genes within anthocyanin molecules.

Aquatic Ecosystems

Most of the water on our planet is in the oceans that cover 71 percent of Earth's surface. Less than 1 percent of all the water is considered freshwater, and most of that is frozen in the polar ice caps. The study of freshwater aquatic **ecosystems**, limnology, has often been separated from the study of marine systems, oceanography. Although freshwater and marine ecosystems are extremely diverse in structure, all of the plants and animals must live in or on water. The physical constraints and opportunities for life in water, and how all of these living organisms interact with each other in a liquid medium, give a unifying theme to aquatic studies.

ecosystem an ecological community together with its environment

The Influence of Water

Water is a liquid and has a greater density and viscosity than air. It can absorb a large amount of solar radiation with a small increase in temperature. Once heated, it will get cooler at a slower rate than land. Aquatic organisms are therefore somewhat buffered against massive, rapid changes in temperature. Aquatic organisms, however, may have to adapt to the water temperature in hot freshwater springs, to the hot vents in the ocean floor in volcanic areas, and to the chilling cold of the water of the polar oceans and freezing winters in the temperate zones of the world. Cold water is denser than hot water, and this may lead to massive mixing and turnover in lakes. In rivers and streams, the water depth and the water flow rate will determine the structure of the biological communities. Plants have to be attached and be highly specialized in structure to survive in fast-flowing water. In larger bodies of water, such as lakes and oceans, wind and tides will mix waters and carry sediments and organisms over large distances. Wave action will alter the physical structure and the geography of shores and coastlines and have a tremendous effect on the biological communities that can survive there.

Water is not always clear, and photosynthetic plants are limited to growing on or near the water surface, or in shallower coastal zones where they can receive sufficient sunlight. While marine habitats all have high levels of salts, the nutrient ion content and the alkalinity and acidity (pH) of freshwater habitats are variable. Plants in water need to get all of their mineral nutrients from the water or from the sediment below. They must also find sufficient oxygen and carbon dioxide to respire, photosynthesize, grow, and reproduce.

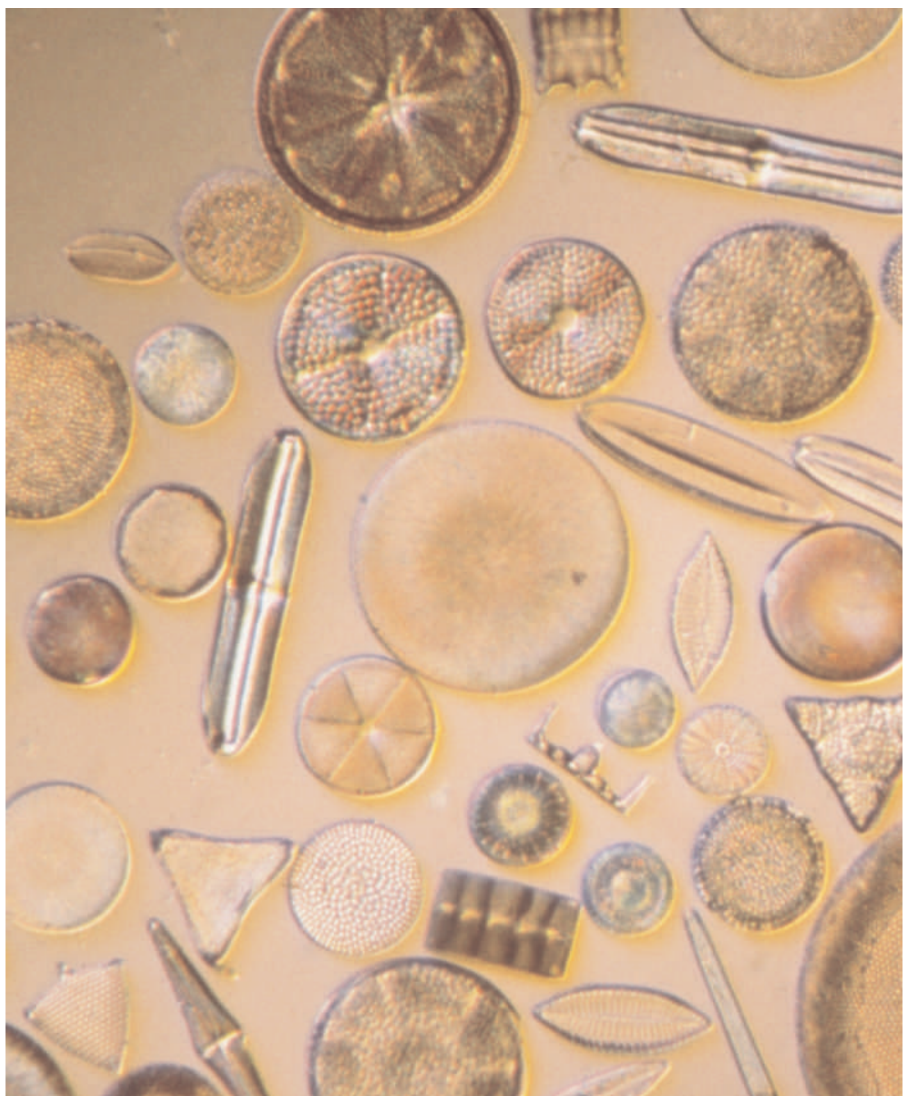
Diversity of Habitats

In both freshwater and marine ecosystems, the majority of the photosynthetic plants are algae. Most of these algae are microscopic. Huge colonies of algal cells, however, can be seen as algal blooms and colonies of **filamentous** forms are easily observed in patches on rocks and in slow-

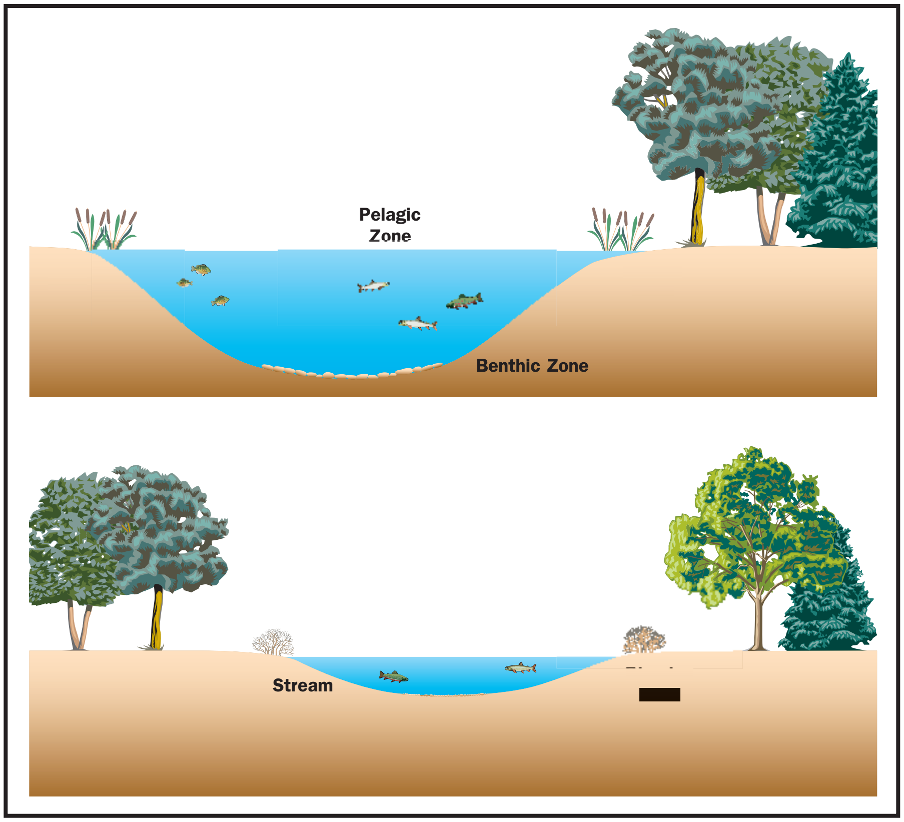
filament a threadlike extension

moving streams. In oceans, microalgae form a major part of the plankton. This phytoplankton is pelagic, living freely in the seawater. Large plants (macrophytes) are less common in oceans, although huge mats of large, floating algae are found in the Sargasso Sea in the mid-Atlantic. Forests of large algae (seaweeds) and some flowering plants (sea grasses) are confined to shallower coastal habitats. These macrophytes are generally attached to rocks or sand on the ocean bottom: they are benthic organisms. Rivers, lakes, and other freshwater habitats contain benthic or pelagic flowering aquatic plants, ferns, mosses, and liverworts that have reinvaded the water from the land at various times during their evolution. In rivers and streams, the water depth and the water flow rate will be a key determinant of plant success. In oceans, currents and tides will carry sediments and organisms over large distances.

All of the aquatic plants are primary producers. Their ability to fix carbon dioxide into carbohydrates by their light-driven photosynthetic reactions makes them the basis of the aquatic food chain. They are grazed upon and eaten, and, when they die, their structures are degraded by a huge variety of dependent organisms in the food web. These freshwater and ma-



A variety of phytoplankton or floating algae. In both freshwater and marine ecosystems, the majority of the photosynthetic plants are algae.



Various aquatic ecosystem zones: pelagic (open water), littoral (shoreline), benthic (freshwater), and riparian (riverbanks).

rine organisms will include fish and other strictly aquatic organisms as well as bacteria, fungi, birds, and mammals that are related to land-living forms.

Freshwater aquatic ecosystems are very diverse. They include lakes, ponds, rivers, and streams with a wide range of depth, flow rates, and water chemistry. Aquatic ecosystems include wetlands, where the water is either just below or just above the soil surface. The depth and distribution of this water may change with season. Wetlands are termed bogs, fens, swamps, and marshes. These have been extensively catalogued depending upon the position of the **water table**, the water chemistry, and the plant communities that grow in them.

water table level of water in the soil

Aquatic ecosystems are not isolated from the adjacent land nor from each other. The inputs and exchanges of sediments, water, and organisms are continuous. The marine shoreline—the littoral zone—is particularly rich in species and has a clearly visible **zonation** of organisms and habitats from the land into the sea. A similar habitat zonation is seen on the shore of a lake. Riverbanks—the riparian zone—will have a specialized plant **community** influenced by the amount of shading by trees on shore. These interactions between freshwater and marine ecosystems are seen both in estuaries, where rivers flow into the sea, and in coastal salt marshes.

zonation division into zones having different properties

community a group of organisms of different species living in a region

Apart from this wide variety of natural aquatic ecosystems, humans continue to build and develop a large number of artificial aquatic ecosystems. These range from reservoirs, canals, channels for irrigation and drainage, and paddy fields for the production of rice, through lakes and ponds built for landscaping and fish culture, down to the decorative home aquarium. The understanding and management of these natural and artificial aquatic ecosystems, together with the need to slow the destruction and move to restore many of the natural areas, will continue to challenge us all. Human populations have always lived close to water. The ecosystems on seacoasts, by lakes, and in the river valleys are under tremendous pressure from **urbanization**, industrialization, and commerce. SEE ALSO Algae; Aquatic Plants; Coastal Ecosystems; Ecosystem; Wetlands.

urbanization increase in size or number of cities

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Aquatic Plants

All land plants have evolved from aquatic ancestors. Species from nearly one hundred flowering plant families, along with some ferns, mosses, and liverworts, have reinvaded the water. Many land plants can tolerate flooding for some time. A good definition of aquatic plants is therefore difficult. The term is normally used for plants that grow completely underwater or with leaves floating on the surface. Parts of the shoot, particularly flowering stems, will often grow up above the water. Most aquatic plants live in freshwater—in lakes, ponds, reservoirs, canals, or rivers and streams. These habitats are very different in water depth, flow rates, temperature, acidity and alkalinity (**pH**), and mineral content. Some aquatic plants live in river mouths, with an ever-changing mixture of fresh- and saltwater, and a few (such as sea grasses) live completely submerged in the sea. Aquatic plants can be free-floating (e.g., water hyacinths) or rooted to the bottom of the pond or stream (e.g., water lilies). The most important grain crop in the world, rice, is an aquatic plant.

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral; low pH numbers indicate high acidity; high numbers indicate alkalinity

Water supply is generally not a problem for aquatic plants. They do not need waterproof **cuticles** or a lot of woody tissue to keep them erect. Life underwater, however, is a challenge. All green plants need oxygen and carbon dioxide. These gases cannot diffuse easily from the air down through the water. Most of the alterations in **physiology** and structure in water plants are adaptations to solve these gas exchange problems. Many water plants develop large internal air spaces—aerenchymatous tissues—in their roots and shoots. These air spaces make the tissues buoyant and help them float. Green leaves, photosynthesizing underwater in the light, release oxygen that can be temporarily stored in the air space and later used for cellular respiration. If the plant grows or floats to the surface, oxygen can also easily diffuse down through the air spaces. One of the water lilies, *Nuphar*, has even developed a ventilation system to circulate air from the leaves floating on the water surface down to its roots in the mud. The rapid growth of shoots to the surface—called depth accommodation growth—seen in rice seedlings and many other aquatic and amphibious species, is driven by the shoot buoyancy and a buildup of carbon dioxide and the naturally produced gas, ethylene, in the tissues under water. Plant organs in the mud at the bottom of lakes survive long periods without much oxygen.

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

physiology the biochemical processes carried out by an organism

Water hyacinths (*Eichhornia crassipes*) and floating ferns (*Salvinia auriculata*) on Lake Naivasha, Kenya.

Aquatic plants require carbon dioxide for photosynthesis. The amount of carbon dioxide dissolved in water depends on the pH and temperature. Aquatic plants may acidify their leaf surfaces. This causes carbon dioxide to be liberated from carbonate and bicarbonate salts dissolved in the water. Underwater leaves are often finely divided, with a large surface area. Unlike land plants, they may have **chloroplasts** for photosynthesis in the surface cell layer—the epidermis.

chloroplast the photosynthetic organelle of plants and algae

The amount of light available for photosynthesis declines with depth (especially in dirty water), and the light quality (the proportion of red, far-red, and blue light) is also altered. Some species (e.g., *Potamogeton*, *Sagittaria*) can produce underwater, floating, or emergent leaves, each with different shapes and structures all on the same plant—a phenomenon called heterophylly. This is a response to light quality and the amount of a plant hormone, abscisic acid (which is at slightly higher levels in emergent shoots).

Most aquatic plants flower and set seed. Many of them, however, can also grow rapidly and reproduce vegetatively. Aquatic plants, particularly free-floating species, can **colonize** the surface of a water body very quickly. If the water dries up, plants can produce a variety of tubers and resting buds (turions) that will persist in the mud until the water returns. These abilities make aquatic plants some of the most troublesome and persistent weeds in the world, particularly in tropical and subtropical countries. There is, understandably, considerable reluctance to put herbicides into rivers and lakes. A wide variety of control methods, including mechanical harvesting and the introduction of fish and other animals to eat them, have been attempted. The canal system of late nineteenth-century Britain was clogged with introduced *Elodea canadensis;* the water hyacinth, *Eichhornia crassipes*, has spread from tropical South America to waterways in Africa, Asia, and North America; and *Salvinia auriculata*, a free-floating aquatic fern, rapidly covered the 190-kilometer lake behind the Kariba Dam on the Zambezi River in Africa in the 1960s. The Everglades and waterways of the southeastern United

colonize to inhabit a new area

States have been repeatedly invaded by quickly spreading, alien aquatic plants.

Many aquatic habitats, and the aquatic plants that live in them, however, are under constant threat from pollution and from drainage for urban and industrial development across the globe. Aquatic plants can help remove pollutants and purify our water supplies. They are also a vital part of a fully functional aquatic **ecosystem** for fish and other wildlife. SEE ALSO Aquatic Ecosystems; Coastal Ecosystems; Rice.

ecosystem an ecological community together with its environment

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Arboretum

See Botanical Gardens and Arboreta.

Arborist

Arboriculture is the care of trees, shrubs, and other woody plants. An arborist is a professional who cares for these plants. Many career opportunities are waiting for arborists in the tree care industry.

Arborists are people who like to work outdoors with their hands, enjoy helping the environment, take pride in their work, and prefer work that is physically and mentally challenging. Arborists combine physical skills, technical knowledge, and a sincere interest in trees to gain personal satisfaction and earn a good living.

Trees have enormous value. They produce oxygen, filter impurities from the air and water, and help to control erosion. They provide shade and can significantly lower heating and cooling costs. When properly selected, planted, and maintained, they greatly increase property values.

Trees are the largest and oldest living things on Earth. It may seem strange to think that trees need help to survive in urban and suburban conditions. But without regular care, they can quickly change from a valuable resource to a costly burden. That's when the skills of the professional arborist are needed.

Arboriculture involves many types of activities. Arborists select and transplant trees. Arborists prune, cable, fertilize, plant, and remove trees. They treat trees for harmful insects and diseases. In short, arborists ensure that the trees in their care grow well and remain structurally safe so that people can enjoy them for generations to come.

There are arborists who work for cities and towns, utility companies, and colleges and universities. By far, however, the largest employer of arborists in North America is the commercial tree service industry. Commercial arboriculture involves individuals, partnerships, and companies.

A tree trimmer hangs over a tree damaged by Hurricane Andrew at the Fairchild Tropical Garden on Biscayne Bay, Florida.

Commercial arborists work for homeowners, property managers, golf courses, power companies, and government agencies.

Career opportunities in commercial arboriculture across the United States are plentiful. Most employers eagerly accept applications and readily train people with the right attitude. Employers commonly provide on-the-job training for entry-level positions, which means that inexperienced employees can prepare for advancement while they earn a living. Training prepares the fledgling arborist for advancement into such positions as tree climber and crew leader. Promotions into sales or management positions are common.

Specialized training is available at technical and vocational schools and community colleges. Many four-year colleges and universities have programs in arboriculture, forestry, horticulture, plant science, pest management, and natural resources.

Wages and benefits available in arboricultural careers vary widely, depending upon the employer's size, geographic location, and other factors. The National Arborist Association conducted a survey of commercial tree service companies across the United States. It showed that in 1999 the average hourly wage paid to an entry-level employee without an advanced degree was $9.51.

As computers and new electrical tools enter the profession, the need for skilled, educated professionals will grow. Modern arboriculture demands decisions and treatments based on an understanding of a tree's biological and chemical systems. Working with trees offers a unique chance to challenge oneself both physically and mentally.

The arboriculture profession has diverse employment opportunities. Where one starts depends upon attitude, education, and experience. The same opportunity for advancement is available for everyone. With a career in arboriculture, advancement opportunities and potential financial rewards are wide open. Finally, working in the field of arboriculture is stimulating, personally rewarding, and beneficial to the environment. SEE ALSO Forestry; Tree Architecture; Trees.

Peter Gerstenberger

Archaea

morphology shape and form

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

murein a peptidoglycan, a molecule made of sugar derivatives and amino acids

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

flagella threadlike extension of the cell membrane, used for movement

At first glance, members of domain Archaea look very much like Bacteria in **morphology**, but biochemical and evolutionary studies have shown that they are a unique branch of life, separate from Bacteria (Eubacteria) and Eukaryotes. This was first recognized by comparing the sequences of their ribosomal deoxyribonucleic acid (DNA) and their type of cell wall to those of other organisms. Although Archaea also have a **prokaryotic** cell organization, other differences set them apart from Bacteria. While most Archaea have cell walls, they do not contain **murein** as in Bacteria, but are made of a number of different molecules, including proteins. The lipids found in their cell membranes are also different from those found in Bacteria and **eukaryotes**. Archaea can be motile by rotating **flagella**, but the proteins that make up the flagella are different from those found in Bacteria. Archaea have a number of traits that make them more similar to eukaryotes than to Bacteria. For example, in Archaea ribonucleic acid (RNA) polymerases and other proteins involved in making RNA from DNA are more similar to those in eukaryotes than those in Bacteria. Because of these and other similarities to eukaryotes, Archaea are thought to be the ancestors of the nuclear and cytoplasmic portions of eukaryotes.

Archaea include many organisms that live in extreme environments or that have unique metabolisms. These include methanogenic (methane-making) Archaea, halophilic (salt-loving) Archaea, extremely thermophilic (heat-loving) sulfur metabolizers, and thermoacidophiles, which live in acidic high-temperature environments.

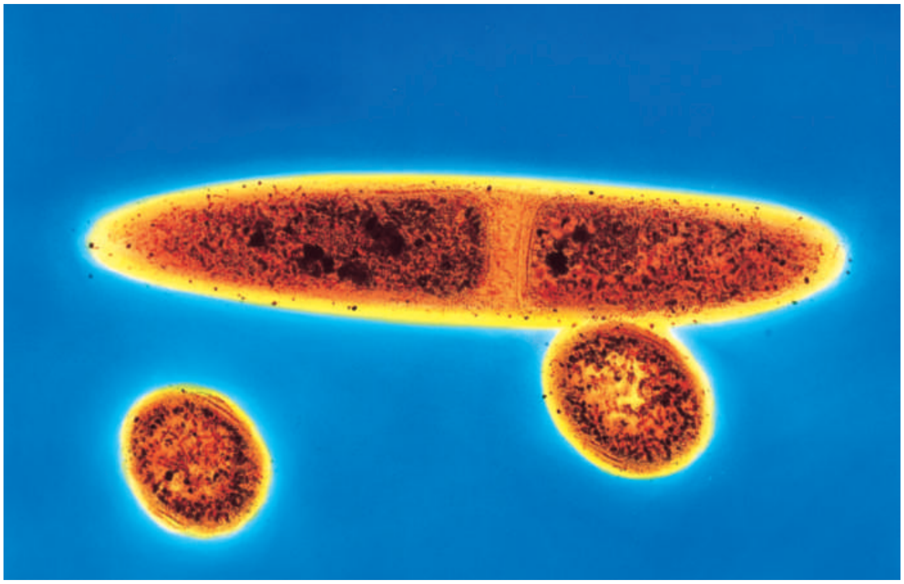
anoxic without oxygen.

Methanogens are killed in the presence of oxygen and live in **anoxic** places, such as the muds of rice fields and the guts of animals, particularly insects and cows. They produce methane, or natural gas, which is used by humans as a source of energy.

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

Halophiles can only live in places with very high salt concentrations, much saltier than the open oceans. They contain a pigment similar to one found in human eyes, bacteriorhodopsin, which allows them to use light energy to make adenosine triphosphate (**ATP**). Carotenoid pigments, which help shield the cells from damaging ultraviolet (UV) light, make the cells appear orange-red. High-salt aquatic areas containing many halophilic Archaea can be seen from a distance because of this red color.

Thermoacidophiles are a group of Archaea that can live in very acidic environments at elevated temperatures. They are found in hot springs such



Colored transmission electron micrograph of the archaea *Methanospirillum hungatii* undergoing cell division.

as those in Yellowstone National Park, volcanoes, burning coal piles, or at undersea hydrothermal vents. Many of them use sulfur compounds for their metabolism. Some are hyperthermophiles, organisms that live at the highest temperatures known (between 80° and 113°C). They are even found living in boiling water.

Because Archaea inhabit extreme environments that were probably prevalent on the early Earth, some believe that they are an old group of organisms (hence their name) that may hold clues to the origin of life. However, extreme thermophiles have also been found among the Bacteria, and Archaea have been shown to be abundant in more moderate environments as well. Environmental studies using DNA survey techniques (PCR) show that low-temperature Archaea make up a significant portion of the prokaryotic **biomass** in terrestrial and planktonic marine environments. From these types of environmental PCR studies, which can tell us what kind of organisms are present in the environment without relying on traditional methods of culturing, we know that both Archaea and Bacteria are abundant in the biosphere, and that the majority of these organisms and their ecological role have yet to be described and understood. SEE ALSO Eubacteria; Evolution of Plants.

biomass the total dry weight of an organism or group of organisms

J. Peter Gogarten and Lorraine Olendzenski

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Arecaceae *See Palms.*

Asteraceae

Asteraceae (or Compositae), the sunflower family, is the largest family of flowering plants, encompassing some fifteen hundred **genera** and nearly

genera plural of genus

Open faces of sunflowers in Norfolk, England.

twenty-five thousand species. Most species are herbs, but some are shrubs and a few are trees. They are of worldwide distribution and are often conspicuous in their habitats. Members of the family share a distinctive flowering structure, consisting of numerous small flowers (often called florets) that are tightly clustered into a head. The five petals of a floret are fused to form a corolla tube that encloses the stamens and **pistil**. Florets that have all evenly sized petals are called disk florets. Florets that have fused petals expanded greatly on one side into a long strap are called ray florets. A typical head consists of numerous disk florets in the center and a row of ray florets around the margin. The strap-shaped corollas of the ray florets project outward, giving the entire head the appearance of a single, large flower (e.g., sunflowers, *Helianthus annuus*). Some members of the family have heads with only disk florets (e.g., ironweeds, *Vernonia* spp.), and some have all florets with strap shaped corollas (e.g., dandelions, *Taraxacum officinale*). A few members have the florets and heads greatly reduced and are wind pollinated (e.g., ragweeds, *Ambrosia* spp.).

pistil the female reproduction organ

Despite the size of the family and its wide distribution, only a few members have become economically important crops, such as lettuce (*Lactuca serriola*), artichokes (*Cynara scolymus*), sunflowers (*Helianthus annuus*), chicory (*Cichorium intybus*), and pyrethrum (*Tanecetum cinerariifolium*, an insecticide). Some species are notable weeds (e.g., dandelions) and some, like sagebrush (several species of *Artemisia*), dominate the landscape where they occur. Many species are cultivated as garden ornamentals, and some use their generic names as common names, for example, aster, chrysanthemum, dahlia, gaillardia, and zinnia. SEE ALSO ANGIOSPERMS; DICOTS; FLOWERS; INFLORESCENCE.

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Atmosphere and Plants

Plant distribution and health is controlled by properties of the atmosphere such as climate, hurricanes, lightning, and pollution. Plants also play a large role in controlling the atmosphere. In fact, the atmosphere at any one location is not only the result of global atmospheric weather patterns, it is also the end result of the type and amount of vegetation.

Effect of Plants on Climate

Over the course of a day, the bulk of energy from the Sun is used in one of two processes: raising temperatures or changing water from a liquid or solid state to vapor form. (Photosynthesis uses only about 2 percent of the Sun's energy.) If a large amount of vegetation is present and is actively conducting photosynthesis, most solar energy is used to convert liquid water in leaves to water vapor. This release of water vapor from leaves is called transpiration. If there is no vegetation, as after a logging clear-cut, evaporation can take place from the soil, but much more energy is used to increase temperatures. Therefore, clear-cutting large forests can significantly raise temperatures. In the Amazon forest in South America, the process of transpiration produces high humidity in the atmosphere, which in turn is then returned to Earth as rain. As much as half of the precipitation in the western Amazon is from this recycled moisture. In these and other ways, plants influence the climate in their region. The type of vegetation also affects the radiation budget, that is, the percent of solar radiation that is reflected back into space; for instance, sparsely vegetated areas reflect more light than densely vegetated areas.

Plants and Atmospheric Oxygen

Forests—in particular, the tropical forest—are often called the lungs of the planet. It is true that plants produce oxygen during photosynthesis, but they and the organisms living in their **ecosystems** also consume about the same amount of oxygen during respiration. Oxygen makes up 21 percent of Earth's atmosphere but annual production of oxygen by plants is only about .05 percent of the atmospheric amount. There is so much atmospheric oxygen that completely destroying all vegetation would have only a minor effect on atmospheric oxygen levels. Doubling the amount of vegetation would increase atmospheric oxygen by only .5 percent. So it is not true that plants are responsible for our global oxygen supply, at least in the short term. Other processes relating to the weathering of rocks and oceanic circulation operating at the timescale of tens of thousands of years are principally responsible for regulating oxygen levels. Plants are, however, very important in the cycling of carbon dioxide.

ecosystem an ecological community together with its environment

Plants and Volatile Organic Compounds

Easily evaporated **compounds** containing hydrogen and carbon are known as volatile organic compounds (VOCs). There are thousands of VOCs in the atmosphere, and plants produce many of them. Monoterpenes and isoprenes are the best-known plant-produced VOCs. Most monoterpenes are produced by conifers in leaves, wood, and bark. Once produced, monoterpenes stay in the plant tissue and are used by plants for defense

compound a substance formed from two or more elements

Mist shrouds plants in the rain forest near Limoncocha, Ecuador.

herbivore an organism that feeds on plant parts

against **herbivores**. Isoprene, produced by deciduous trees, spruces, and mosses, does not stay in the plant. The production of isoprene helps plants conduct photosynthesis at high temperatures that would otherwise be very damaging. Production of other VOCs gives many plants their characteristic aroma.

VOCs also react quickly in the atmosphere. In the presence of nitrogen oxides and sunlight, VOCs react to form ozone, a major component of smog. In urban areas, industrial activity and the use of cars can produce very high levels of nitrogen oxides. This, combined with the production of VOCs by plants, can be a major contributor to urban pollution. In cities with large forest populations, such as Atlanta, Georgia, plant-produced VOCs can account for a large portion of the urban smog problem. Human activities, however, are still responsible for the bulk of urban smog as well as the production of the large amounts of nitrogen oxides reacting with the VOCs. In Switzerland, a highly industrialized country, plant-produced VOCs made up only 23 percent of total VOCs. Trees should therefore not be blamed for most smog.

Air Pollution and Pollution-Tolerant Plants

Our industrial society produces large amounts of pollution. Sulfur dioxide is produced by the combustion of a variety of high sulfur fuels, especially coal. Acid rain is produced from sulfur dioxide. Aluminum and glass factories produce fluoride, a pollutant that can accumulate in plants. Ozone and peroxyacetyl nitrate, both produced in the presence of sunlight, nitrogen oxides, and VOCs, are major components of smog and together are the most serious air pollution problem faced by plants.

Pollution enters the plants through stomata, tiny pores used by leaves for gas exchange. Yellow or brown coloration along leaf edges and veins are signs of pollution damage. Cell membranes are destroyed and the biochemical reactions of photosynthesis are slowed or stopped. Air pollution itself does not usually kill plants, but it can severely reduce crop yields and makes plants more susceptible to diseases and insects. The damage created by pollution depends on the concentration of the pollutant as well as on the duration of the pollution event. For example, long-term exposure to low pollution levels may be less damaging than short, intense pollution events. Long-term processes such as acid rain, though, can damage forests by changing soil acidity over many years.

Plants vary greatly in their ability to resist pollution. In some cases, plants are resistant to sulfur dioxide, but not to ozone. In Australia, *radiata* pines are usually more resistant to sulfur dioxide than broadleaf eucalyptus trees. Yet in Sweden, broadleaf trees resist ozone better than the conifers. There is also tremendous variation in ozone resistance within the *Eucalyptus* genus. Sweeping generalizations about individual species are virtually impossible, but plants do seem to follow several patterns:

- thick leaves are pollution-resistant
- species or varieties that have high rates of stomatal conductance (the process that brings carbon dioxide and pollution into the leaf) experience more pollution damage
- plants can often adapt to high pollution over time
- older plants are more resistant than younger plants.

For most species that have been studied, botanists can develop plant varieties that are resistant to a certain pollutant or combination of pollutants. Therefore it is usually better to assess local pollution problems and to select or breed plant varieties for that situation than it is to identify universally resistant species. SEE ALSO Acid Rain; Carbon Cycle; Defenses, Chemical; Global Warming; Human Impacts; Photosynthesis, Carbon Fixation and; Terpenes; Water Movement.

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Auxins

See Hormones.

B

Bamboo

Bamboos are members of the grass family (Poaceae). Like other grasses, bamboos have jointed stems, small flowers enclosed in structures known as spikelets, a specially modified embryo within the seed, and a grainlike fruit. However, bamboos are the only major group of grasses adapted to the forest habitat, and they differ from other grasses in having highly scalloped photosynthetic cells in their leaves. Many bamboos have tall, somewhat arched stems, but others are shrubby, or slender and **twining**, and some resemble ferns. The largest bamboos reach 30 meters (100 feet) in height and 30 centimeters (12 inches) in diameter, while the smallest ones have delicate stems no more than 10 centimeters (4 inches) tall.

twining twisting around while climbing

There are at least twelve hundred known species of bamboos worldwide, which occur from 46°N (Sakhalin Island, Russia) to 47°S (southern Chile), although most are tropical or warm temperate. Bamboos often grow at low elevations, but many species grow in mountain forests, and some range up to 4,300 meters (14,200 feet) elevation in equatorial highlands. Woody bamboos (**tribe** Bambuseae), with at least eleven hundred species, make up the bulk of bamboo diversity: these are the plants normally thought of as bamboos. The woodiness of their stems is derived entirely from primary growth, and although there are other woody grasses, the Bambuseae are the only major group of grasses characterized by woodiness. Approximately one hundred species of tropical, herbaceous, broad-leaved grasses (tribe Olyreae) are closely related to their woody cousins, and these are now also classified as bamboos. Bamboos are typically associated with Asia, but close to one-half of their diversity is native to Central and South America, and there is one species (giant cane, or switch cane) native to the southeastern United States.

tribe a group of closely related genera

Woody bamboos are ecologically important in the tropical and temperate forests where they grow. Rapid elongation of bamboo shoots, tall, hard stems, and profuse vegetative branching allow woody bamboos to compete with trees for light. Woody bamboos easily **colonize** forest edges and gaps by means of vegetative reproduction through their well-developed underground stems (rhizomes), whereas herbaceous bamboos are characteristic of the shady forest floor. The large **biomass** of bamboo stems and leaves provides an excellent habitat for a wide variety of animals, including beetles and other insects, birds, monkeys, frogs, rats, and pandas.

colonize to inhabit a new area

biomass the total dry weight of an organism or group of organisms

Woody bamboos are well known for their unusual flowering behavior, in which the members of a species grow for many years (up to eighty or more) in the vegetative condition, and then flower at the same time and die after fruiting. Other flowering behaviors are documented in bamboos, but many exhibit this periodic, gregarious type of flowering, and the effect on the forest is dramatic when it occurs. Large areas of bamboo plants die back, providing openings for recolonization by the forest while the bamboo seeds sprout and start the next generation. How bamboo plants count the passage of time, or what triggers the gregarious flowering, is unknown.

In Asia, where a bamboo culture has existed for several thousand years, bamboos are a symbol of flexible strength, and they are an integral part of daily life. Young, tender bamboo shoots are a tasty vegetable, whereas the mature stems are used in construction, scaffolding, fencing, and bas-

A bamboo grove at Haleakala National Park on Maui, Hawaii.

ketry or for paper pulp. Mature stems are also fashioned into utensils, water pipes, musical instruments, and a multitude of other items. Bamboo is an important theme in Asian artwork, and bamboos frequently are used as a material for artwork. Bamboos are also widely planted as ornamentals in many parts of the world. The utility of bamboo is exploited wherever it is cultivated or grows naturally, and there is increasing recognition of the potential of bamboo as a renewable resource, especially for reforestation and housing. SEE ALSO Economic Importance of Plants; Grasses; Monocots.

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Bark

vascular related to transport of nutrients

meristem the growing tip of a plant

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

Bark is the outer protective coating of the trunk and branches of trees and shrubs and includes all the tissues outside of the **vascular** cambium. A typical bark consists of several layers of different types of tissue. The inner bark, or bast, is living and contains the conductive tissue, called phloem, by which sugars are transported from the leaves in the crown of a tree to the roots, and from storage tissues to other parts of the plant. The outer bark is layered, with the inner layer consisting of the cork cambium, a **meristem** that produces cork cells to the outside. The cork cells are usually tightly packed and have fatty substances deposited in their thick walls. In contrast to the cork cambium, cork cells are dead and filled with air, making cork lightweight and insulating.

The appearance of a bark depends on the type of cork cells produced by the cork cambium, the relative amount of cambial products, and the amount of secondary conducting tissue (phloem). In some species, such as the cork oak (*Quercus suber*), the cork cambium is very active and produces a thick layer of cork, which is extracted and used commercially. Other species, such as birch trees, have a papery bark because the cork cambium alternatively produces several layers of thin-walled cells. These are fragile, and the thicker layers can come off as sheets. In habitats where natural fires occur, such as tropical savannas and the pine and redwood forests of California, trees tend to have a thick, corky bark to insulate them from the heat of fires. In some arid regions many trees have chlorophyll-containing bark to continue the process of photosynthesis when the leaves are absent during long periods of drought. The varied texture and thickness of bark is often a function of the environment in which the tree grows. The variation in the structure of bark often gives a tree its characteristic appearance, for example, the hairy look of the shagbark hickory. A forester can recognize the species of trees by the differences in their bark either externally or by cutting a small slash to examine the inner structure.

Bark is used in many ways and is of considerable economic importance. Many indigenous peoples have made clothes, canoes, houses, drinking vessels, arrow poisons, and medicines from bark. Bark has also provided commercial medicines such as quinine and curare, and is also the major source of **tannins** for the leather industry and cork for wine bottles. In horticulture, bark is used for mulch. Some of our favorite flavors and spices, such as cinnamon and angostura bitters, come from bark. Bark is much more than the protective skin of trees; it is one of the most useful products of nature. SEE ALSO STEMS; TISSUES; TREE ARCHITECTURE; TREES.

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Bessey, Charles

American Botanist
1845–1915

Charles Edwin Bessey was a late nineteenth- and early twentieth-century American botanist who developed a modern classification system for flowering plants. Born in Ohio in 1845 the son of a school teacher, Bessey was educated at home and in small rural schools. He was able to attend the Michigan Agricultural College, where he was introduced to botany. After graduation, he helped to initiate the botany program at the Iowa Agricultural College, and began teaching students. He made advances in botany education by adding a laboratory component to his classes. He used his one microscope initially to teach his students during laboratory. Later, as he helped to start botany programs at other state colleges in the American west, he introduced microscope techniques to botany classes there as well.

In 1872 Bessey worked at Harvard in American botanist Asa Gray's (1810–1888) laboratory and became more interested in the microscopic characteristics of plants. His examinations of cell structure and organization led to the publication of several papers on plant diseases. He further contributed to American botany education by writing an American version of German plant physiologist Julius von Sachs's *Lehrbuch der Botanik* that he called *Botany for High Schools and Colleges.*

Bessey's most important publication, however, was probably *Phylogenetic Taxonomy of Flowering Plants*, published in 1915, the year of his death. This last major work of Bessey's established the phylogenetic system of organizing flowering plants that taxonomists are still building on today with the use of genetic techniques. In this publication, Bessey proposed new evolutionary relationships between plants. Previously, it was thought that plants that had flowers without petals were the most primitive. Bessey instead suggested the opposite. He believed what is still thought to be true now, that the most primitive, original flowers had many separate petals and stamens and carpels. As flowering plants evolved, these **whorls** of flower parts fused together, or were reduced or became absent in some species. This indicated that flowers such as *Ranunculus*, or buttercup flowers, were the more primitive, while tiny flowers such as those hanging in **catkin inflorescences** in some trees were more advanced. This also implied that monocotyledonous plants, such as grasses, had evolved from dicotyledonous broad-leaved plants. These ideas led to a big change in principles for plant taxonomy, and they encouraged a new wave of research into plant phylogeny.

whorl a ring

catkin a flowering structure used for wind pollination

inflorescence an arrangement of flowers on a stalk

Bessey worked in many ways to promote science and the study of plants. In addition to his great contributions to taxonomy, Bessey was also part of many scientific societies. He was a member of the American Association for the Advancement of Science, and served as its president in 1910. He participated in the Iowa Farmers' Institute, which was the first institute of its kind in the country. Bessey was also associate editor of prestigious journals, such as the *American Naturalist* and *Science*. Bessey will remain best known, however, for his contribution to a detailed and modern plant phylogenetic system. Botany students still study the branching tree diagrams of plant evolutionary relationships like those Bessey proposed in 1915. SEE ALSO Evo-

lution of Plants; Gray, Asa; Phylogeny; Sachs, Julius von; Taxonomist; Taxonomy.

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Biodiversity

gymnosperm a major group of plants that includes the conifers

population a group of organisms of a single species that exist in the same region and interbreed

ecosystem an ecological community together with its environment

Biodiversity exists at three interrelated levels: species diversity, genetic diversity, and community-level diversity. When we talk about plant biodiversity, we refer to the full range of plant species, the genetic variation found within those species, and the biological communities formed by those species. For vascular plants, biodiversity includes all species of ferns, **gymnosperms**, flowering plants, and related smaller groups such as clubmosses and horsetails. The genetic variation found within **populations** and among populations arises through the mutation of individual genes or chromosomes and is rearranged by genetic recombination during the sexual process. Genetic variation is important not only for the survival and evolution of species; it is also important to people for breeding improved crop plants with higher yields.

Biological diversity also refers to all biological communities, including temperate forests, tropical forests, grasslands, shrub lands, deserts, freshwater wetlands, and marine habitats. Each of these biological communities represents an adaptation of plants to particular regimes of climate, soil, and other aspects of the environment. This adaptation involves **ecosystem** interactions of each biological community with its physical and chemical environment. For example, the ability of a forest community to absorb rain water and slowly release the water into streams and the ability of a swamp to process and detoxify polluted water are both aspects of ecosystem-level biological diversity that are of central importance to human societies.

Measuring Biodiversity

Biological diversity can be measured in various ways, each of which captures some of the overall meaning of biological diversity. The most common method of measuring biological diversity is simply to count the number of species occurring in one particular place, such as a forest or a grassland. Since it is not possible to count every species of plant, insect, fungus, and microorganism, the usual procedure is to count certain types of organisms, such as birds, butterflies, all flowering plants, or just tree species. This type of local diversity of species is usually referred to as species richness or alpha diversity. A tropical rain forest might contain three hundred or more tree species in a square of forest measuring 400 meters on a side, whereas a temperate forest of equal area might contain only forty tree species. Biological diversity can also be measured in larger areas. For example the country of Colombia has more than fifty thousand species of higher plants, in contrast to sixteen hundred species for the United Kingdom and nearly sixteen thousand for Australia. This type of regional or large-scale diversity is referred to as gamma diversity.

Bialowieza National Park in eastern Poland displays great biodiversity of species. Covering 312,000 acres, it is the last primeval forest in Europe, with some of its trees more than 600 years old and 100 feet tall.

Another way to measure biodiversity is to consider the number or percentage of a region's species that are **endemic** to that region. For example, of the United Kingdom's fifteen-hundred native plant species, only sixteen species or 1 percent are endemic. The overwhelming majority of the United Kingdom's plants can be found in other neighboring countries, such as Ireland, France, and Germany. In contrast, 14,074 of the 15,000 plant species of Australia are endemic and found in no other country.

endemic belonging or native to a particular area or country

Individual species can also be compared for their evolutionary uniqueness. Species that are not closely related to other species are generally considered to have greater value to overall biological diversity than species that have many close relatives. For example, the maidenhair tree, *Ginkgo biloba*, is the only species in its genus, and *Ginkgo* is the only genus in the gymnosperm family Ginkgoaceae. In contrast, the common dandelion, *Taraxacum officinale*, has many related species in the same genus and is a member of a large family, the Asteraceae, with twenty-five thousand species and eleven hundred genera. Using this approach, a species that was the only member of its genus and family would have greater biodiversity value than a species that had many relatives in the same genus and belonged to a family with many genera. In contrast, a few biologists would argue that a species in a large genus has greater value because this species has the greater potential to undergo further evolution than a species with no close relatives that may be an evolutionary dead end.

U.S.A.	**19,473**	**United Kingdom**	**1,623**	**India**	**16,000**	**China**	**32,200**
Canada	**3,270**	**France**	**4,630**	**Indonesia**	**24,375**	**Japan**	**5,565**
Mexico	**26,071**	**Congo**	**11,007**	**Australia**	**15,990**	**Philippines**	**8,931**
Chile	**5,292**	**Tanzania**	**10,008**	**New Zealand**	**1,628**		
Colombia	**51,220**	**Madagascar**	**9,505**	**Papua New Guinea**	**11,544**		
Peru	**18,245**	**South Africa**	**23,420**				

Number of species of higher plants in selected countries.

Extent of Diversity

There are around 250,000 living species of higher plants in the world today. Of these species, the overwhelming majority are flowering plants. Flowering plants are grouped into more than three hundred families, including such large and economically important families as the Poaceae, which contains the grasses and the cereal crops we depend on for food and animal fodder; the Fabaceae, which includes the beans and peas we need for protein in our diet; and the Rosaceae, which is important for fruit trees and ornamentals such as apples, pears, and roses.

Higher plants exhibit a great diversity of growth forms, leaf shapes and sizes, flower and fruit types, seed types, and particular adaptations for growing in different environments. Growth forms include trees, shrubs, annual herbs, perennial herbs, climbers, and aquatic plants.

Plant diversity is not equally distributed across the world's surface. Only a relatively few land plants are adapted to salt water, and these are found rooted in shallow waters. So the large oceanic expanses of the world are devoid of higher plants. On the land surface, the greatest diversity of plants is found in the tropical lowland and **montane** rain forests of the Americas, central Africa, and Southeast Asia. In such forests there is a great diversity of plant species in the form of trees, shrub, herbs, and climbers. There is also an abundance of **epiphytes**, in particular orchids and bromeliads, that perch on the branches of the trees. Illustrating this tropical diversity, there are only around thirty tree species in all of northern Canada, in contrast to

montane growing in a mountainous region

epiphytes plants that grow on other plants more than one thousand tree species in just the southern countries of Central America.

There is also great species diversity in the temperate regions of the world that have mild, wet winters and dry, hot summers, such as the Mediterranean basin, the California region, central Chile, the cape region of South Africa, and southwest Australia. In such areas, many plants have adaptations to drought, such as **succulent** cacti, which store water in their stems, and annual plants that grow, reproduce, and die in one growing season.

succulent marked by fleshy, water-holding leaves or stems

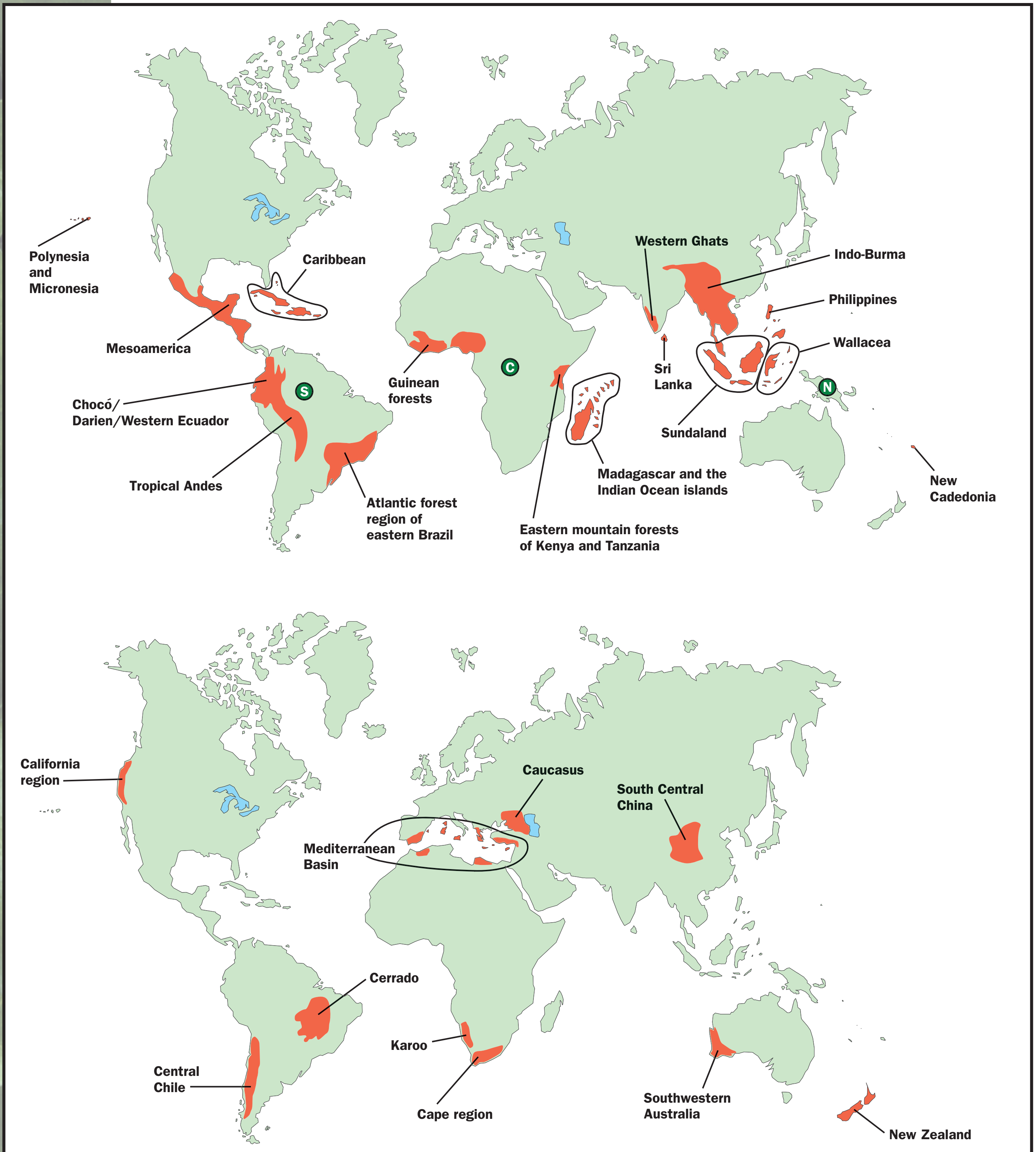
Certain regions of the world are known as hot spots of biodiversity because of their high concentrations of species overall, their high percentages of species that are endemic, and the high degree of threat that those species face. In addition to rain forest areas and localities with Mediterranean climates, many of these are islands, such as the Caribbean Islands, Madagascar and nearby islands, New Caledonia, New Zealand, Sri Lanka, and the islands between New Guinea and peninsular Malaysia. Biodiversity hot spots encompass the entire range of 44 percent of the world's plant species, 25 percent of the bird species, 30 percent of the mammal species, 38 percent of the reptile species, and 54 percent of the amphibian species on only 1.4 percent of Earth's total land surface. The premier hot spot is the tropical Andes, in which 45,000 plant species, 1,666 bird species, 414 mammal species, 479 reptile species, and 830 amphibian species occur in the tropical forests and high-altitude grasslands that occupy less than 0.25 percent of Earth's land surface. This approach can also be applied to individual countries. In the United States hot spots for endangered species occur in the Hawaiian Islands, the southern Appalachian Mountains, the arid Southwest, and the coastal areas of the lower forty-eight states, particularly California, Texas, and Florida.

Threats to Biological Diversity

Biological diversity is being lost today at all levels, including genetic variation, species, and biological communities. The most serious threat is the extinction of species, because once a species is lost, it can never be regained. The loss of genetic variation is occurring in two different ways: when populations of a species are eliminated and when populations become smaller in size. This loss of populations is seen most immediately in the local extinction of species. In a study of a conservation area in Massachusetts, one-third of the native plant species present one hundred years ago could no longer be found today. They were not replaced by other native species, but there was an increase in the number of nonnative species. This park is now poorer in total species, and many species still present have fewer populations. Many species that were formerly listed as common now have only a few individuals left.

Biological diversity is most severely threatened when entire biological communities are lost. In many tropical countries of the world, the tropical rain forests that are so rich in species have been largely destroyed. Examples of countries with devastated forests are Madagascar (87 percent lost), Rwanda (84 percent), Vietnam (83 percent), and the Philippines (94 percent). With the loss of these communities comes the extinction of plant and animal species, the loss of genetic variation within remaining species, and the loss of the **ecosystem** services provided by these communities, such as

ecosystem an ecological community together with its environment



At top, fifteen tropical rain forest hot spots of high endemism and significant threat of imminent extinctions. The circled areas enclose four island hot spots: the Caribbean, Madagascar and Indian Ocean islands, and the Sundaland and Wallacea regions. The Polynesia/Micronesia region covers a large number of Pacific Ocean islands, including the Hawaiian Islands, Fiji, Samoa, French Polynesia, and the Marianas. Circled letters indicate the only three remaining tropical forest wilderness areas of any extent: S = South America, C = Congo Basin, N = New Guinea. The bottom map indicates ten hot spots in other ecosystems. The circled area encloses the Mediterranean Basin. Redrawn from Primack, 2000.

flood control, soil erosion protection, and the production of wood and food. Other habitats almost completely destroyed include tropical deciduous forests, of which more than 98 percent have been destroyed in Central America, and temperate grasslands, which are readily converted to agriculture and ranching. In the United States, only around 560 acres of the tallgrass prairie of Illinois and Indiana remains undisturbed, only about one ten-thousandth of the original area. Wetlands including swamps, bogs, floodplains, and **vernal** pools are similarly suffering devastation. As these habitats are damaged by human activity and converted to other uses, the species they contain decline in abundance and eventually become extinct. Habitats that are restricted in area and contain high concentrations of endemic species are particularly vulnerable, such as the rain forests of Hawaii and isolated mountain peaks in the southwestern United States.

vernal related to the spring season

In general, the rate of extinction for plants has been lower than that for animals. To date, there are recorded extinctions of around four hundred plant species, about 0.2 percent of the total in contrast with around 2.1 percent of mammals and 1.3 percent of birds already extinct. The lower percentages of plants that are extinct are related in part to our ability to protect small populations of plants in nature reserves. In contrast, many animals have a greater need to migrate and have often been extensively exploited. At the turn of the twenty-first century, around 9 percent of plant species are in danger of extinction, a figure only slightly lower than that for birds (11 percent) and mammals (11 percent). The extinction rates for certain groups of plants are much higher than this average value. For example, 32 percent of gymnosperms and 33 percent of palms are threatened with global extinction in the wild due to the limited distribution of many species' specialized habitat requirements and the intensive collection of plants for horticulture.

Factors Threatening Species

Species are threatened with extinction primarily because of habitat destruction. Species are also driven to extinction when their habitat is degraded to the point where they can no longer exist. This might happen when a grassland is heavily grazed by domestic animals, a forest is repeatedly logged, or uncontrolled fires burn shrub land. Fully 81 percent of the endangered species of the United States are threatened by habitat degradation and loss. Species are also lost from habitats fragmented by human activity, when habitats are broken up into smaller pieces by roads, fences, power lines, residential areas, and ranches. The remaining fragments may be so altered in micro-climate, and so much more vulnerable to other human activities, that many plant species are no longer able to survive.

The second most significant threat to species diversity is competition and **predation** from exotic invasive species, which is a threat for 57 percent of the endangered plant species of the United States. In many cases, exotic species of animals such as cattle, sheep, goats, rabbits, and pigs selectively remove certain native plant species. For example, pigs introduced in Hawaii have removed all wild individuals of numerous plant species. Invasive exotic plants have often overwhelmed natural communities and outcompeted the native species. For example, in bottomland communities of the southern United States, Japanese honeysuckle plants have replaced the rich wildflower

predation the act of preying upon; consuming for food communities, and in the rangeland of the western United States European grasses outcompete native grasses and wildflowers. As a result, native species decline at the expense of the introduced species.

Overharvesting of plants, often for food, medicinal purposes, or by horticulturists, threatens 10 percent of the endangered plant species of the United States. A notable example is ginseng, an herb used in Asian medicine, which has been so overharvested throughout its range that only a small number of plants remain. Many rare wildflowers, such as orchids, have been so severely overcollected by gardeners that they are in danger of extinction in the wild. Information on the location of the last remaining plants is often kept secret to prevent the theft of these individuals.

compound a substance formed from two or more elements

mutualism a symbiosis between two organisms in which both benefit

Pollution threatens 7 percent of the plant species of the United States. Water pollution can alter the water chemistry so severely that aquatic plants cannot grow. Increased inputs of nitrogen and phosphorus **compounds** into the water from sewage and agricultural fertilizers can result in algal blooms that shade out and kill native plants. In the land environment air pollution in the form of smog, acid rain, and nitrogen deposition can cause plants to slow down in growth or die. In some cases, this death may be related to the decline and death of the sensitive soil fungi (mycorrhizae) that have **mutualistic** relations with plants, providing water and mineral nutrients and receiving carbohydrates in return. And lastly, about 1 percent of plant species is threatened by disease and parasites. While this number may not seem very great, some of the most important woody plants in the forests of North America, such as chestnuts, elms, and dogwoods, are in severe decline due to introduced diseases.

What Can Be Done?

The most important way to protect plant biological diversity is to establish protected areas that include high concentrations of species, particularly those species in danger of extinction or in decline. These protected areas may be established by governments, conservation organizations, or private individuals. Management plans must be developed and implemented, and these protected areas must be monitored to ensure they are meeting their goals. Many management plans for protected areas include some forms of public education, because public support is often crucial for the success of a park.

Where it is not possible to maintain plant species in the wild due to ongoing threats, plants can often be grown in botanical gardens or kept as stored seed samples in seed banks. Networks of botanical gardens and seed banks are making a concerted effort to increase their holdings of endangered species and species of potential agricultural and economic importance. The goal of many botanical gardens is to increase knowledge of plants, to educate the public concerning plants, and to return plants eventually to their natural habitats.

The diversity of plant species provides us with the agriculture crops that are our food, many of the medicines that keep us healthy, wood that is needed in construction, fodder that feeds our domestic animals, ornamental plants that enrich our gardens and homes, and even the oxygen that we breathe. People could not live without the diversity of plants, and many plant species will live in the wild only if we take care of them. SEE ALSO

Asteraceae; Botanical Gardens and Arboreta; Endangered Species; Gingko; Human Impacts; Invasive Species; Rain Forests; Seed Preservation; Wetlands.

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Biogeochemical Cycles

Nutrients are elements that plants require for growth. In most terrestrial **ecosystems**, a lack of essential nutrients may limit plant primary productivity. Net primary productivity (NPP), other ecosystem processes, and ecosystem structure and function may be best understood by examining and studying the cycles of these nutrients. To trace the movement of a nutrient—such as nitrogen (N), phosphorus (P), sulfur (S), or carbon (C)—as it travels between the living (biotic) and nonliving (abiotic) components of an ecosystem is to trace its biogeochemical cycle.

ecosystem an ecological community together with its environment

The Phosphorus Cycle

A generalized biogeochemical cycle of phosphorus, for example, starts with its release from apatite (phosphorus-containing rock). Inorganic, plant-available forms of phosphorus in most soils derive from apatite. Mechanical and chemical weathering reactions release phosphorus from apatite into the soil solution. Plants take up available forms of phosphorus, such as orthophosphate ($H_2PO_4^{3-}$), from the soil solution into their roots. After uptake from the soil, phosphorus travels as the phosphate anion HPO_4^{2-} through the plant before accumulating in leaves and other living tissues. Phosphate is present in plant cells and circulating fluids at a concentration of about 10^{-3} m. Plants also incorporate inorganic phosphate into organic forms that may be used for various metabolic processes. Because there are no gaseous forms of phosphorus and soil reserves are small, phosphorus is difficult for plants to acquire. As a result, plants hoard phosphorus. Rather than releasing it back into the environment, plants send the phosphorus to the roots for storage before dropping their leaves. This process, called **translocation**, ensures that the plant will have a sufficient supply of phosphorus for the next growing season. Any phosphorus remaining in the dead leaves falls to the ground in leaf litter. This phosphorus gradually returns to the soil organic matter after microorganisms, such as fungi and bacteria, break down the litter through decomposition, and the cycle commences again.

translocate to move, especially to move sugars from the leaf to other parts of the plant

The time that it takes for the phosphorus to move from apatite into the soil solution is called the flux rate. This represents the amount of time it takes a given amount of a certain element to move between the pools, or reservoirs. Flux rates can be very slow or very rapid. It may take hundreds of years for the phosphorus in the apatite to move into the soil solution. In contrast, once plant-available phosphorus is in the soil solution it is rapidly taken up by the plant roots. The mean residence time (MRT) is the length of time that elements remain in a pool. The MRT for phosphorus in apatite may be thousands of years, but within a plant, the MRT may be only one year. Nutrients move between pools through meteorological, geological, hydrological, biological, or **anthropogenic** mechanisms.

anthropogenic human-derived

Transport Mechanisms

Meteorological mechanisms of nutrient transport are generally related to precipitation in the form of rain, fog, snow, or ice. For example, nitrogen has various gaseous phases including ammonia (NH_3) and nitrous oxides (NO_x). The nitrogen-containing gas may dissolve in precipitation, whereupon the nitrogen is subsequently deposited on plant and soil surfaces. In contrast, phosphorus, which has no gaseous phase, is not incorporated in rain but may be transported as dust by wind currents through the atmosphere. Nutrients also move slowly over the long term (hundreds of thousands of years) and over long distances via geological mechanisms, such as **sedimentation**, **uplift**, and volcanism. For example, carbon (C) may be stored in combination with calcium (Ca) as calcium carbonate ($CaCO_3$) in seashells. The shells fall to the ocean floor and through sedimentation processes become calcite, or calcium carbonate rock. Over thousands or millions of years, this carbon may be released slowly to the atmosphere from near-shore sedimentary rocks. Eventually, the nitrogen deposited on the land by precipitation and the carbon released from the calcite become incorporated into organic matter, the biological component of ecosystems.

sedimentation deposit of mud, sand, shell, or other material

uplift raising up of rock layers, a geologic process caused by plate tectonics

Biological mechanisms generally refer to the microbial transformations of elements that are stored in organic matter into inorganic forms of nutrients that may be used by plants. For example, soil bacteria and fungi release acids that break down leaf litter and release the phosphorus and nitrogen that are bound in it. The phosphorus and nitrogen then combine with oxygen or hydrogen to form plant-available **compounds**.

compound a substance formed from two or more elements

Biological mechanisms of nutrient distribution can also include movement of nitrogen or phosphorus from one area to another via mammals or birds. Studies of bison movement in Oklahoma's tallgrass prairie ecosystem show that, when nitrogen-containing bison fecal pats decompose due to fire or chemical breakdown, they create a spatially patchy distribution of soil nitrogen; this patchiness of nitrogen may influence plant distributions. Likewise, a trip to the Caribbean island chain Los Roques, off the coast of Venezuela, provides a striking example of phosphorus distribution by seabirds. Guano, the white bird droppings that coat the island's rock outcrops, contains some of the highest phosphorus concentrations in the world.

Humans are probably the most important biological **vectors** for nutrient transport on Earth, particularly for carbon, nitrogen, sulfur, and phosphorus. Anthropogenic combustion of fossil fuels releases carbon dioxide

vectors carriers, usually carriers who are not affected by the thing carried

(CO_2) to the atmosphere in quantities that exceed the combined releases of CO_2 from plant, animal, and microbial respiration, natural forest and grassland fires, and volcanic emissions. This has contributed to the build-up of CO_2 in Earth's atmosphere and may alter the biogeochemical cycles of other elements. Fossil fuel combustion also releases nitrogen and sulfur, which ultimately contributes to the formation and deposition of acid rain. Mining of phosphorus, such as in Los Roques, has altered the long-term storage of phosphorus, increased the flux rate of the global phosphorus cycle, and contributed to the phosphorus pollution of freshwater ecosystems worldwide. These and other human activities are altering the biogeochemical cycles of nitrogen, phosphorus, sulfur, and carbon at the global scale, with largely unknown consequences for Earth's inhabitants and ecosystems. SEE ALSO BIOGEOGRAPHY; CARBON CYCLE; NITROGEN FIXATION; NUTRIENTS.

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Biogeography

Biogeography is the study of the patterns of distribution of the world's living organisms. It tries to determine where plants and animals occur, why they occur where they do, and when and how the patterns developed. Biogeographic patterns are largely determined by climate, geology, soil conditions, and historical events. Individual plant species are generally restricted to particular habitats, but many plants have widely overlapping ecological requirements so that many different kinds grow together in communities.

Impact of Climate

Rainfall has a significant impact on the distribution of plant types. Savannas, steppes, and prairies occur where rainfall patterns result in long, dry periods at certain times of the year. During the dry season, fires often sweep through these areas. Woody plants, with buds for future vegetative growth borne above ground, are killed by the flames. Grasses and other herbaceous plants, whose reproductive buds are produced on underground shoots, and, therefore, protected from fires survive and thrive. Where annual rainfall is greater and more uniform throughout the year, fires are less frequent and woodlands develop. In contrast, deserts develop where rainfall is severely limited.

Vegetation is also influenced by temperature and length of growing season. In the Arctic, where the ground is frozen for several months of the year and the growing season is measured in weeks, only a relatively few, specialized species of dwarf plants are able to grow. Diversity under such conditions is considerably less than in the tropics, where annual temperatures

A Montana tallgrass prairie in summer.

and rainfall often remain favorable, and the growing season extends throughout the year. Trees in the tropics can grow to a large size and provide further habitats for **epiphytic** plants and animals among their branches in the forest canopy.

epiphytes plants that grow on other plants

Other Factors

While climate is a major force in determining the patterns of biogeography, other factors are also important, including the **physiological** requirements and tolerances of individual species. Although many plants overlap in their ecological tolerances, they all vary from each other. Individual species of plants rarely occur continuously in the landscape to the exclusion of all others. For instance, the red maple (*Acer rubrum*) in eastern North America is a plant of acid soils and commonly grows with other wetland species in lowlands from eastern Canada to Florida and from the Atlantic to the Mississippi, but it can also grow on dry ridges and hilltops with a different association of plants within the same geographic region. When we examine the distribution of red maple carefully, we also see that the individual plants are not continuous, but occur only where growing conditions are favorable. Some individuals may occur next to each other, but others live some distance away. The individuals within a reasonably close distance to each other, and which are capable of interbreeding, are called populations. Populations, just like individuals, may occur next to each other or be widely separated. Populations occurring far from the main range of distribution of a species are generally referred to as disjunct populations, or simply as disjuncts.

physiology the biochemical processes carried out by an organism

Highly specialized habitats such as bogs, barrens, rock outcrops, and **vernal** pools, which themselves occur in a scattered fashion across the landscape, are frequently home to disjunct species that are especially adapted to those particular ecological conditions. These habitats can be further divided by soil types. Barrens may occur over serpentine, limestone, sandstone, granite, and other less common types of rocks, and each supports a different group of plants particularly adapted to that specific habitat. One particular

vernal related to the spring season

plant that has a wide distribution in North America from the southeastern United States to eastern and central Canada is the pitcher plant (*Sarracenia purpurea*). When the populations are plotted on a map the species appears to have a continuous distribution throughout its range, but in reality, individual populations occur only in scattered, highly acidic, boggy situations.

Intercontinental Disjunctions

Looking at the distribution of plants today, we see it only as a single slice of time. Studying historical data, we find a very different picture of the position of continents and the distribution of plants and animals. One of the most challenging problems faced by biogeographers is to explain intercontinental disjunctions, in which closely related plants are found on opposite sides of the world from each other and separated by major oceans. One intercontinental disjunction that has attracted particular attention is the one between eastern Asia and eastern North America. About seventy-five **genera** of plants are restricted to these two areas and occur nowhere else in the world. These plants have no or few close relatives in their respective regions, and there is no confusion over their close relationship to their disjunct sister **taxa**. Swedish botanist Carl Linnaeus first noticed that closely related plants grew in these two areas in 1750, but it was not until Asa Gray published a series of papers between 1840 and 1860 that this disjunction was brought into prominence. In fact, Gray's series of papers, which were written in response to requests by Charles Darwin for statistics on the North American flora, are often considered to be the seminal papers in the field of biogeography.

genera plural of genus

taxa a type of organism, or a level of classification of organisms

The genera belonging to this pattern often occur in what are considered to be ancient **lineages**, and include Magnoliaceae, Berberidaceae, Schisandraceae, Illiciaceae, Hamamelidaceae, and Saururaceae, but some more modern groups such as Rubiaceae and Asteraceae also contain a few genera with close relatives on opposite sides of the world and nowhere else. Gray tried to explain this pattern by proposing migrations across a Bering land bridge connecting the Asian and American continents during periods when sea levels were lower and corridors for migration were available in the center of North America. This was a simple and plausible explanation, but in reality the origin of this pattern of distribution has proven to be much more complex.

lineage ancestry; the line of evolutionary descent of an organism

Later, the German botanist Adolf Engler (1844–1930), in writing about the vegetational history of Earth, made use of rapidly accumulating fossil evidence, particularly from the Arctic, to show that the forests in which these disjunct plants now occurred had once been more widespread and continuous at higher latitudes in the northern hemisphere: they essentially circled the globe in a zone where boreal forests now exist. Engler believed that deteriorating climates and the uplifting of mountains worldwide, and increasing aridity in the western part of North America, led to the extinction of this vegetation type in large portions of the world during the latter portion of the **Tertiary period**. (This group of plants is still frequently referred to as the **Arcto-Tertiary geoflora**.) It was also believed that the Pleistocene glaciations of the last two million years further contributed to the extinction of many of the plants in North America and Europe. It has been postulated that the major east-west mountain ranges in Europe—the Pyrenees, Alps, Carpathians, and Balkans—would have blocked the migration of plants in front of the southwardly moving ice sheet, thereby resulting in extinc-

Tertiary period geologic period from sixty-five to five million years ago

Arcto-Tertiary geoflora the fossil flora discovered in arctic areas dating back to the Tertiary period; this group contains magnolias (*Magnolia*), tulip trees (*Liriodendron*), maples (*Acer*), beech (*Fagus*), black gum (*Nyssa*), sweet gum (*Liquidambar*), dawn redwood (*Metasequoia*), cypress (*Taxodium*), and many other species tion. In contrast, north-south ranges, such as the Appalachians, allowed southerly migration and survival.

Many of the plants and animals restricted to eastern Asia and eastern North America today are known from fossils in Europe and western Asia, and geological evidence indicates that the Bering land bridge was not the only route available for migration between Eurasia and America. Until about forty-nine million years ago and perhaps as recently as about thirty-seven million years ago, North America, Greenland, Iceland, and Europe existed close enough to each other to allow direct migration of plants and animals across the North Atlantic. At that same time, the connection across the Bering Straight was also at a higher latitude than it is today, and climate may have been a controlling factor in plant and animal migrations. It is interesting to note that many genera of plants—*Magnolia*, *Liriodendron*, *Juglans*, *Sassafras*, *Acer*, and so forth—that now occur primarily or have their greatest diversity in eastern and southeast Asia and eastern North America are known from the Miocene of Iceland. According to Malcolm McKenna in the *Annals of the Missouri Botanical Garden* (1983), the closest relatives of Iceland's plants at that time were in North America. Since the end of the Pleistocene glaciations, the composition of Iceland's flora has become more European in character.

Island Biogeography

biota the sum total of living organisms in a region of a given size

Islands require special examination. In a sense, islands are like isolated laboratories where long-term experiments in adaptation and evolution are taking place. Many factors have to be considered to understand the origin and development of an island's **biota**. Such factors include size and elevation of the island, latitude, distance from nearest landmass, age of the island and how long it has remained above sea level, past connections to mainlands, source of migrants, frequency of arrival of new colonists, wind direction, and rainfall patterns. Extinctions and recolonizations, too, have to be analyzed to understand the biological patterns present on islands.

Hawaii and the Galapagos Islands are classic examples where processes of island biogeography have been studied. Hawaii has never been connected to another landmass but instead sits over one of Earth's geological hot spots. As the Pacific plate moves to the west-northwest in conveyor belt fashion, new islands are created as magma flows up through Earth's crust to form volcanoes that eventually reach far above sea level. Activity of the hot spot is apparently intermittent, since the volcanoes are separated by gaps of varying sizes. As the islands move away from the hot spot, they are gradually eroded by the elements and eventually consumed as the Pacific plate dives under the Asian continent. This process has been going for at least seventy million years. Since the islands were barren at their creation, the plants and animals on the Hawaiian islands must have originally come from elsewhere. The nearest major landmasses to Hawaii, and the most likely sources of plant and animal colonists, are more than 4,000 kilometers away.

speciation creation of new species

The first colonists to reach Hawaii would have encountered a rich diversity of wide-open ecological niches ranging from sea level to the tops of mountains (some of which exceed 4,000 meters). The diversity of unoccupied habitats is thought to have promoted rapid **speciation**. Because of the great distance from the major sources of colonists, the number of successful colonizations is estimated to be only 270 to 280 species of plants. These have evolved to about 1,000 native species today, although some botanists who place greater emphasis on minor variations consider the number to be much higher. The Hawaiian flora is also considered to be disharmonious, meaning its species distribution differs from that of similar mainland regions. For example, only three native orchids are found on Hawaii, although one would expect many more because of the archipelago's tropical location and wide range of habitats. Conversely, the Campanulaceae (bluebell family) is the most **speciose** family in the islands, with 110 species of native plants. In other regions of the tropics, the family is an insignificant portion of the flora. SEE ALSO Biodiversity; Evolution of Plants; Gray, Asa; Orchidaceae.

speciose marked by many species

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Biomass Fuels

Biomass fuel is fuel produced from organic material of recent biological origin. Biomass suitable for the production of fuels is classified as either biomass waste or energy crops.

biomass the total dry weight of an organism or group of organisms

Biomass waste is any material of recent biological origin that has been discarded because it has no apparent value. Examples of biomass waste include residues from agricultural crops, municipal solid waste, and even sewage. Because this waste originates from biomass that recycles to the environment on a nearly annual basis, it is a sustainable energy resource; that is, the resource will be available for future generations.

Energy crops are defined as plants grown specifically as an energy resource. An energy crop is planted and harvested periodically. The cycle of planting and harvesting over a relatively short period assures that the resource is used in a sustainable fashion. Energy crops include woody crops harvested on a rotation of five to seven years and herbaceous energy crops harvested on an annual basis. Examples of woody crops include **hybrid**

hybrid a mix of two species

poplars and willows. Examples of herbaceous crops include switchgrass and sweet sorghum. Peat moss is also harvested and used as a fuel.

Solid fuels such as biomass are at an enormous disadvantage when compared to petroleum and natural gas because they are more difficult to transport and handle. The goal of many biomass conversion processes is to convert solid fuel into more useful gaseous or liquid forms. Gaseous fuels can substitute for natural gas in machinery to produce heat and power. Liquid fuels can substitute for gasoline or diesel fuel in automobiles and trucks. Both gaseous and liquid fuels can also be used to produce chemicals and materials currently made from petroleum resources.

anaerobic without oxygen

Either **anaerobic** digestion or thermal gasification can produce gaseous biomass fuels. Anaerobic digestion is the decomposition of organic solids to gaseous fuel by bacteria in an oxygen-free environment. The product is a mixture of methane, carbon dioxide, and some trace gases. Thermal gasification is the conversion of solid fuels into flammable gas mixtures consisting of carbon monoxide, hydrogen, methane, nitrogen, carbon dioxide, and smaller quantities of higher hydrocarbons.

Liquid biomass fuels can be produced from solid biomass by three processes: fermentation to ethanol, processing of vegetable oils to biodiesel, or thermal processing to pyrolysis oils. Pyrolysis is the high-temperature decomposition of organic compounds in the absence of oxygen to produce liquids. The mixture of oxygenated hydrocarbons is similar to that found in fuel oil.

compound a substance formed from two or more elements

Fermentation is the decomposition of complex organic molecules into simpler **compounds** by the action of microorganisms. A variety of carbohydrates (such as sugars, starches, hemicellulose, and cellulose) can serve as feedstock in ethanol fermentation as long as they can be broken down to sugars that are susceptible to microbial biological action. Cellulose and hemicellulose found in the plant cell walls of woody and herbaceous energy crops can also be converted to fermentable sugars, but the process is relatively difficult.

Vegetable oils from soybeans, peanuts, and other grains and seeds can be used as fuel in diesel engines after chemical modification to improve their combustion properties. SEE ALSO AGRICULTURE, MODERN; FORESTRY; OILS, PLANT-DERIVED; PEAT BOGS.

Robert C. Brown

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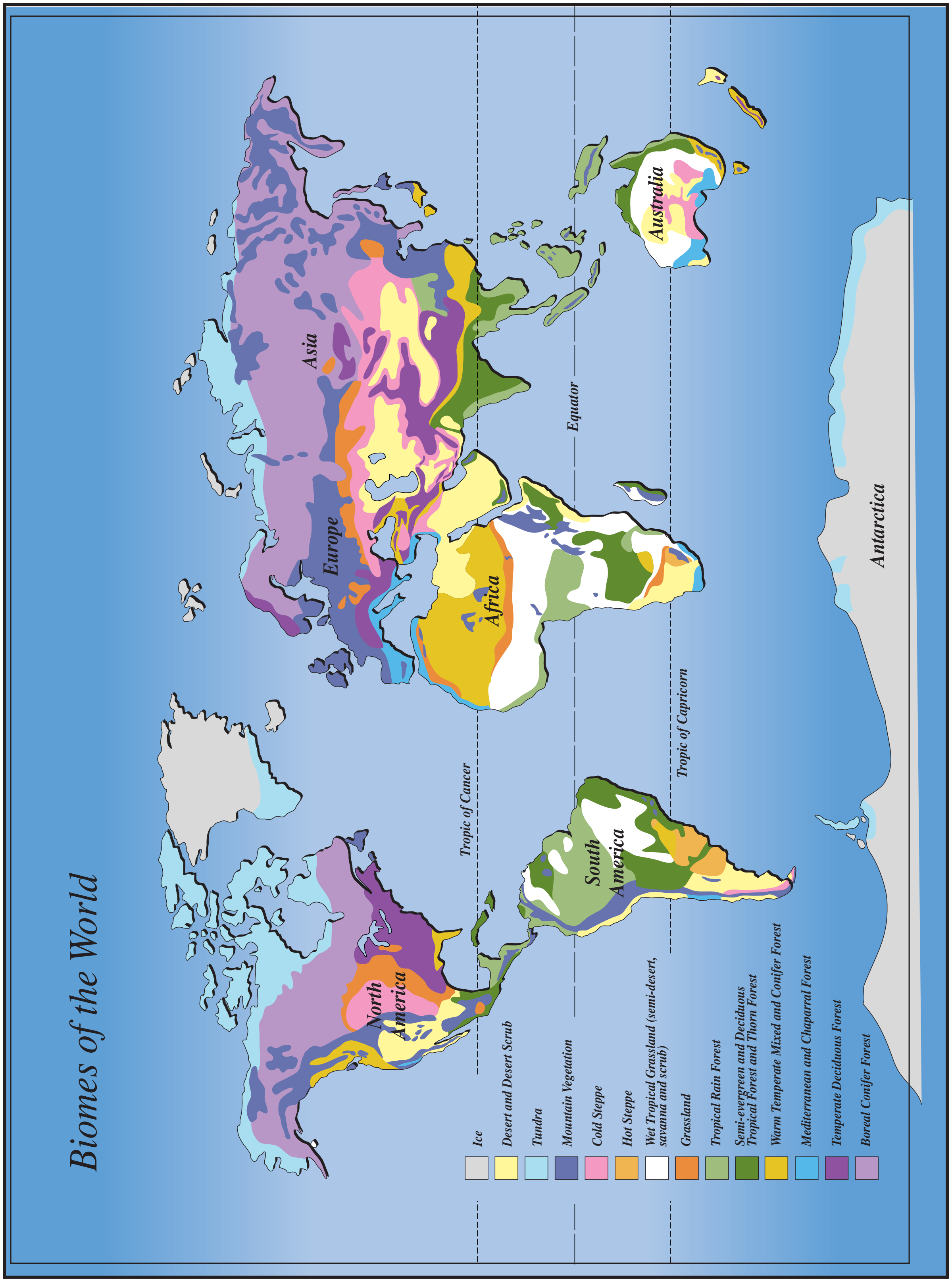
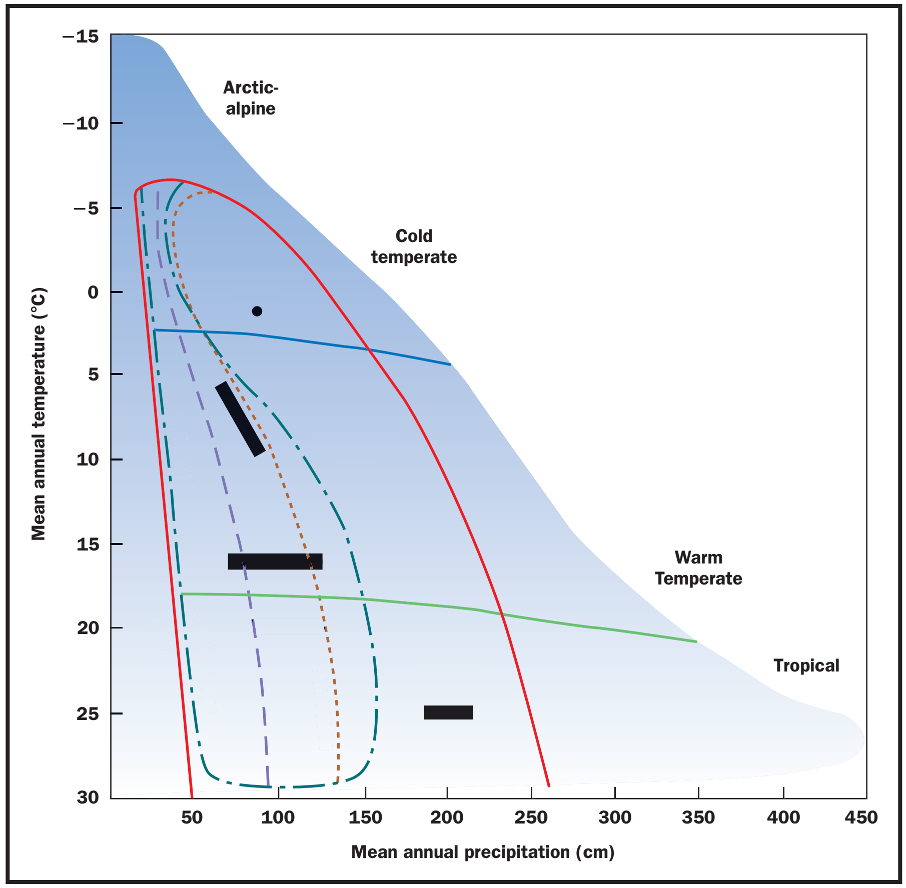
Biome

biogeography the study of the reasons for the geographic distribution of organisms

A biome is a particularly useful **biogeographic** unit that results from large-scale climatic patterns. A portion of a biome, such as the tropical rain forest found in the Amazon basin, may cover thousands of hectares. It will have


Biomes of the World
North America
South America
Europe
Africa
Asia
Australia
Antarctica
Tropic of Cancer
Equator
Tropic of Capricorn
Ice
Desert and Desert Scrub
Tundra
Mountain Vegetation
Cold Steppe
Hot Steppe
Wet Tropical Grassland (semi-desert, savanna and scrub)
Grassland
Tropical Rain Forest
Semi-evergreen and Deciduous Tropical Forest and Thorn Forest
Warm Temperate Mixed and Conifer Forest
Mediterranean and Chaparral Forest
Temperate Deciduous Forest
Boreal Conifer Forest



Mean annual precipitation and temperature of biomes. *Source:* Reprinted from Aber and Melillo, 1991, p. 16.

recognizable vegetation features that impart a sameness that defines the unit. The fact that this region differs from others, such as the desert biome, is evident to even the most untrained observer. Frederic Clements (1874–1945) and Victor Shelford (1877–1968) observed in 1939 that not only was the vegetation characteristic, but that these were plant–animal formations with associated fauna. In the 1960s an ecological research effort, the International Biological Program, sought to characterize the structure and function of major biomes through intense study. American botanist and ecologist Robert Whittaker (1920–1980) summarized some characteristics of the biomes in his book *Communities and Ecosystems*, in which he arranged them graphically according to interacting gradients of mean annual temperature and moisture availability (see accompanying figure).

The Influence of Rainfall

You can bring this model to life though observation as you travel within the continental United States. The Interstate Highway System allows easy movement across the country along latitudes, parallel to the equator, or the longitudes, perpendicular at the equator. Travel on Interstate 80 from New York City to San Francisco during the summer growing season reveals an obvious gradient of change in vegetation. The deciduous forests of central New York State are lush green in most years, with trees predominating where human development has not occurred. In the Midwest, traveling from Illinois into Iowa and Nebraska, the trees are absent except along rivers, and grasses and broad-leaved nonwoody **forbs** cover the landscape like a carpet.

forbs broad-leaved, herbaceous plants

Much of this region is now dominated by fields of grain such as corn and wheat, **domesticated** replacements of the native vegetation that once was predominant in the grasslands. (Remnants of the native prairie are rare.) In August, the green prairies begin to show some signs of the golden color of mature fields as the various annual grasses produce seeds that will ultimately produce plants for the following year. Meanwhile the perennials will die back to ground level by late fall, and then start growth again the following year.

domesticate to tame an organism to live with and to be of use to humans

The farther west one travels, the sparser the vegetation and the less luxuriant the crops, until dry short-grass prairies merge into deserts and badlands with more widely spaced plants and soil that is frequently bare. The predominant color throughout the year in the deserts tends toward earth tones of beige and brown with small green leaves being less evident. Two major north-south mountain barriers, the Rocky Mountains and the Sierra Nevada range in California, interrupt the gradual transition. In these areas, elevation-dependent differences produce a complex mosaic of vegetation that does not fit the overall pattern. Finally, on the West Coast, moisture-laden air deposits rain on the windward sides of the coastal mountains and abruptly changes the pattern. Lush temperate rain forest vegetation forms a margin along the western edges of California north of San Francisco, just as in coastal Oregon and Washington. Southward, the forests are replaced by coastal shrub lands because rainfall is not sufficient to support extensive forests in most places, and the inland deserts are even closer to the ocean shores. This east-west gradient across the country parallels a decline in moisture availability, the first of two major climatic factors that determine the character of biomes.

The Influence of Temperature

A similar trip along Interstate 75 in January from the Canadian border at Sault Ste. Marie, Michigan, to Florida provides evidence of the second major climatic factor gradient. In northern Michigan, it is likely that the ground will be snow covered most of the month. Ohio and Kentucky can present occasional periods with persistent snow cover; by the time you reach Georgia, however, snow generally disappears shortly after it falls, and Florida has only rain. This gradient is not so much a result of differences in volume of precipitation (the amount of rain or snowfall), but the prevailing temperatures. When the north to south temperature gradient overlays the east to west moisture gradient, the type of biological community that will be supported is determined. Similar interactions of temperature and moisture availability determine the presence of other biomes globally as indicated in the map of their distribution. Toward the poles, Canadian boreal forests change over to tundra and illustrate the results of extending the temperature gradient.

Tropical rain forests occur where the temperature is greater near the equator and daily tropical rains maintain high moisture levels. This tropical region along the equator forms a boundary with the temperature gradients in the Southern and Northern Hemispheres being mirror images of each other. In the tropical forest biomes, there is little seasonal change; the prevailing conditions are wet and warm. Seasonal temperature variation is minimal in regions adjacent to tropical forests, but ultimately at increasing distance from the equator, alternating wet and dry periods produce fluctuations in growth rates in subtropical seasonal forests. This moisture-dependent alternation is different from the temperate biomes covering the United States and Canada where the seasons are produced by the alternation of a cold winter and relatively warmer summer.

The classification of biogeographic areas into biomes is only one of several different methods of organizing terrestrial environments. Michael Barbour, in *Terrestrial Ecosystems*, gives a brief historical review of other classification systems, and Robert Bailey, in *Ecosystem Geography*, updates various ways of classifying the Earth's surface. Barbour uses the term *vegetation types* to classify landscape patterns and points out significant differences between the various subdivisions that can be identified, while Bailey prefers the term *ecoregion* as the unit of subdivision at the level of assemblages of landscapes.

Since the distribution of biomes is dependent on global climate patterns, one may question what impact global climatic change could have on these biogeographic units. A continuation of global warming would change the boundaries by moving warmer conditions closer to the poles.

In addition, the climatic changes do not just involve changes in temperature; they also involve changes in air movement patterns, alteration of temperatures (known as El Niño and La Niña) within the oceans, and storm distributions that change the annual growth of both plants and animals. This is not a new phenomenon on Earth. Cold periods have existed in the past, and biome boundaries have shifted in response. This is known from the pollen record left in lakes and bogs over many thousands of years. The challenge to plants and animals is not so much the extent or duration of expected temperature changes, but the rate of those changes. Vegetation can respond to changes that take hundreds or thousands of years to occur by gradually dispersing into new areas or evolving. It cannot move or reproduce fast enough to adapt to the same changes if they occur over tens or hundreds of years. The total ecologic impact of these potential rapid changes is not currently known. SEE ALSO Aquatic Ecosystems; Biodiversity; Chaparral; Clines and Ecotypes; Coastal Ecosystems; Coniferous Forests; Deciduous Forests; Deforestation; Desertification; Deserts; Ecology; Ecosystem; Global Warming; Grasslands; Plant Community Processes; Rain Forests; Savanna; Tundra.

W. Dean Cocking

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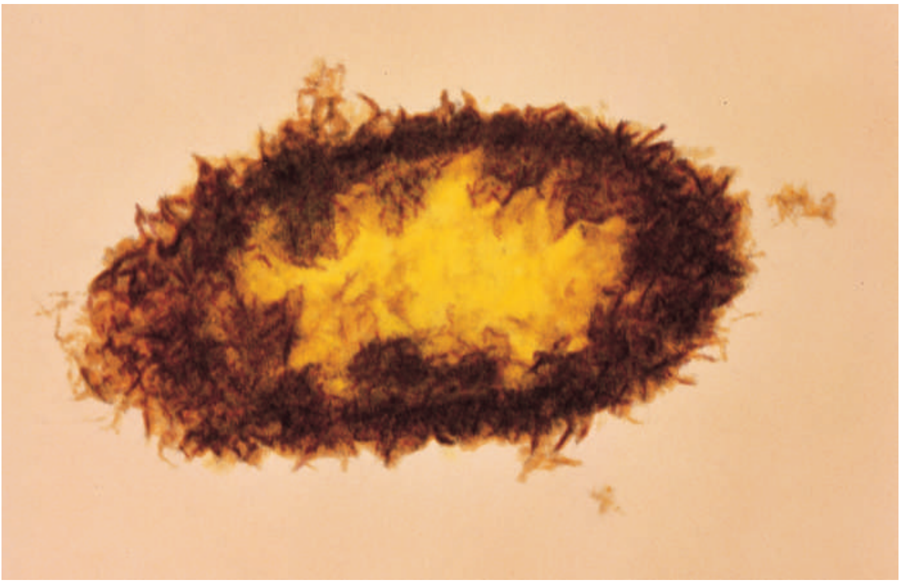
Bioremediation

The word "bioremediation" was coined by scientists in the early 1980s as a term to describe the use of microorganisms to clean polluted soils and waters. The prefix *bio* defined the process as biological, that is, carried out by living organisms. The noun remediation defined the process as one that re-



Desulphovibrio sp., a sulphur-eating bacterium used in toxic waste treatment. In anaerobic conditions such as those found in waste effluents, the bacterium obtains oxygen from sulphate ions. This liberates sulphide ions, which may bond with iron in the waste water to form a precipitate, seen here as the hairlike coating, which attracts toxic metals. The bacterium and its toxic coat may then be isolated by magnetic separation.

sulted in the cleaning, or remediation, of the environment, via complete degradation, sequestration, or removal of the toxic pollutants as the result of microbial activity. Degradation means that the microorganisms decompose the pollutants to harmless natural products such as carbon dioxide (CO_2), water (H_2O), or other nontoxic naturally occurring **compounds**. Sequestration means that the pollutant is trapped or changed in a way that makes it nontoxic or unavailable to biological systems. Removal means that while the pollutant is not necessarily degraded, the microbes physically remove it from the soil or water so that it can be collected and disposed of safely.

compound a substance formed from two or more elements

sequester remove from circulation; lock up

The principal goal of bioremediation is to return polluted environments to their natural state. Examples of the many contaminants that are amenable to bioremediation via degradation include organic chemicals such as pesticides, insecticides, herbicides, and pollutants derived from petroleum as the result of oil or fuel spills, or oil refining activities. Research in the 1990s has shown that even synthetic chemicals previously thought to be totally resistant to degradation, such as the insecticide DDT or the explosive TNT, are, in fact, degradable by microorganisms when they are supplied the right growth conditions. Examples of pollutants that can be **sequestered** or removed by microorganisms include toxic heavy metals such as lead (Pb), cadmium (Cd), and arsenic (As), and radioactive metals such as uranium (U). Toxic levels of metals are found in soils or waters previously contaminated as the result of military, industrial, or mining activities. Metals are found in various chemical forms, but unlike organic compounds, metals cannot be degraded. They can be changed only to some other chemical form. Therefore, the goal of metal bioremediation is to use microbes to change the metals into a form that is either sequestered in the soil in an insoluble form, or changed into a soluble form that can be removed from the soil with water, and then recovered later.

Various processes are used to carry out bioremediation. They include ex situ techniques, where contaminated soil is excavated, bioremediated in a vessel or pile, and then returned to the environment. Alternatively, with

PHYTOREMEDIATION

Phytoremediation uses plants to remove both soilborne and waterborne pollutants. It is proving especially useful for treating heavy metal contamination, an exceptionally difficult type of cleanup job. Plants need soil nutrients and are efficient absorbers of all kinds of minerals. Some species, called hyperaccumulators, can concentrate metals thousand of times above normal levels. Indian mustard (*Brassica juncea*) will hyperaccumulate lead, chromium, cadmium, nickel, selenium, zinc, copper, cesium, and strontium. Detoxifying the soil is as simple as harvesting the plants.

in situ techniques, the contamination is treated where it occurred. This approach is particularly suited to treating contaminated groundwater in deep aquifers. Bioremediation can involve the inoculation of a contaminated environment with the specific microorganisms needed to carry out the bioremediation, or supplementation of the environment with nutrients that will promote the activity of microbes already naturally present. When supplementation is done in situ, it is sometimes called naturally accelerated bioremediation. The microorganisms naturally present in some contaminated environments may sometimes slowly bioremediate that environment without any human intervention. This type of bioremediation is called natural attenuation, a process that usually occurs very slowly over many years. Because it is effective and affordable, bioremediation is often the method of choice for cleaning polluted soils, groundwaters, aquatic areas, wetlands, and other environments. SEE ALSO Human Impacts; Soil, Chemistry of.

Don L. Crawford

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Bonsai

Bonsai is a Japanese word formed by two ideogram characters, the first meaning "pot" or "container" and the second "to cultivate." It is a term that can be applied to any plant grown in a pot. Today it is applied to a tree or shrub grown usually in a ceramic pot, trained or styled by clipping or wiring or both. But it is so much more.

Bonsai is an ancient art form with its origins in China at least as far back as the fourth century. Soon the art spread to Korea and was found in Japan by the sixth and seventh centuries. During the last hundred years the art of bonsai spread and now enjoys worldwide popularity.

Even today, bonsai continues to touch one's soul and intellect with its beauty, tranquility, and natural character of age, just as one would react to viewing a masterpiece of art. Despite its small size, one can sense a large old tree sometimes shaped by wind, often with branches weighed down by imaginary heavy snows, and a sense of balance and perfection in this small plant in a ceramic pot. Bonsai is that ideal tree in nature.

There are two general methods used to transform a plant into a bonsai. A young tree may be grown from seed or from nursery stock. In this case the intent is to concentrate on the development of the trunk by keeping many lower branches. Alternatively, a mature tree may be collected from the field or mountains and then styled.

Care includes almost daily watering and monthly fertilizer applications. Bonsai may be trained into one of many styles. Among them are formal upright (straight trunk), informal upright (curvy trunk), slanted, windswept,

A man shapes and prunes a pine tree bonsai to the desired form.

cascade, multiple trunk, clump, raft, rock planting, broom, raised roots, forest planting, and literati (a variation on the others with sparse branches). Usually, the growth and structural characteristics of the tree determine the style chosen.

Once the plant is selected, the training of bonsai begins with the selection of which side will be the front of the tree, based on the width of the trunk and the sense of stability imparted by the tree. Branches on the left, right, and backside of the plant are then selected and trained. The profile of the tree as seen from all directions, especially the front, is triangular, the corners of which are formed by the apex and the ends of the major left and right branches. Copper or aluminum wire of various sizes is used over a period of several months to bend and hold branches until they retain their position. Highly specialized hand tools are used during this training process. A suitable pot is selected based on how the styled tree harmonizes with the color, shape, width, and depth of the pot. The tree is potted in a coarse or medium well-draining soil mixture.

Several species are more frequently used for bonsai. These include most junipers, pines, and many deciduous or flowering/fruiting shrubs or trees such as the *Prunus* family and azaleas.

It is highly recommended that beginning bonsai enthusiasts receive instruction in styling bonsai since this is more difficult than it sounds.

John Yoshio Naka of the United States is arguably the world's foremost expert in bonsai. He began his bonsai career in Los Angeles, California, in the 1940s. For his accomplishments in bonsai, Naka was recognized with Japan's highest honor for a noncitizen and a national Heritage Fellowship from the U.S. National Endowment for the Arts. At the turn of the twenty-first century he still continued to teach and work on his bonsai daily.

Bonsai can be formally displayed indoors for up to a week. The potted trees are placed on display stands or slabs of finished wood and accompanied with an accent plant that suggests grasses and other plants that typically grow under a tree. Almost all bonsai must be kept outdoors on large tables or individual stands, except during harsh, freezing weather.

Bonsai may be seen in several collections open to the general public. The National Bonsai Foundation has several collections at the National Arboretum in Washington, D.C. Other public bonsai displays are the Pacific Rim collection in Tacoma, Washington, and the Bonsai Pavilion and Garden at the Wild Animal Park in Escondido, California. The Golden State Bonsai Federation has two collections, one at Lakeside Park in Oakland, California, and another at the Huntington Garden in San Marino, California.

Bonsai is an art that will continue to fascinate and amaze people of all races, cultures, and age with its universal appeal. SEE ALSO HORTICULTURE; TREE ARCHITECTURE; TREES.

Sherwin Toshio Amimoto

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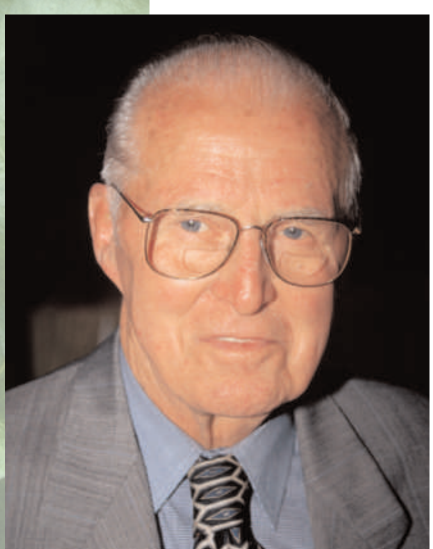
1914–



Norman Borlaug.

Norman E. Borlaug, perhaps the world's best-known plant breeder, was born on a small farm near Cresco, Iowa, in 1914. He studied plant pathology at the University of Minnesota.

In October 1944 Borlaug began work with the Rockefeller Foundation in Mexico. The foundation had begun a new program in Mexico in 1943 aimed at increasing the agricultural yields of the country. Borlaug's primary scientific achievements were as an applied wheat geneticist with the foundation. He oversaw a highly successful use of Mendelian genetics to create new varieties of wheat.

His work involved the identification of parent varieties with useful traits, such as disease resistance and high yield. He then dusted pollen (male reproductive cells) from the flowers of one variety onto flowers from another variety, from which the stamen had been removed. The transferred pollen cells fertilized the ovules (female reproductive cells) of the recipient flowers. The wheat seeds produced by the female parent were harvested and grown into new plants. Borlaug and his team then identified offspring with desired, novel combinations of traits and used them for further crosses. They released offspring offering high promise and reliability to farmers for commercial **cultivation**.

cultivation growth of crop plants

Borlaug used a practice considered controversial at the time: shuttle breeding. This involved shuttling breeding stock between two different geographic regions in order to achieve two crossings per year rather than just one. With this technique, he successfully shortened the time needed to obtain new varieties from about ten years to about five years. His shuttle breeding also enabled him to create new wheat varieties that were widely adaptable. In wheat, this wide adaptability was due in part to eliminating day-length sensitivity (photoperiodism) in flowering.

Borlaug's work was of profound significance. Within ten years, he and his team were able to create varieties of wheat well suited to different regions of Mexico, which enabled Mexican wheat farmers to more than triple production, from 365 thousand tons (750 kilograms per hectare) in 1945 to 1.2 million tons (1,370 kilograms per hectare) in 1956. As a result, Mexico stopped importing wheat and began exporting it.

In 1953 wheat varieties bearing **semidwarfing** genes came to Borlaug from Orville Vogel in Washington State. Vogel had successfully incorporated these genes, obtained from Japanese varieties, into wheats suited to Washington. These varieties responded well to fertilizer and gave substantially higher yields. Borlaug incorporated the semidwarfing genes into his already successful new varieties, which enabled Mexican wheat growers by the early 1960s to obtain over 6,000 kilograms per hectare. In 1963 Borlaug subsequently recommended that India import the new semidwarf varieties, and these plants were equally successful there.

semidwarfing a variety that is intermediate in size between dwarf and full-size varieties

Borlaug's scientific work led to his receipt of the Nobel Peace Prize in 1970. His successes, plus those of his other colleagues in wheat and rice breeding, are often referred to as the Green Revolution. High-yielding varieties of wheat and rice are now grown in all parts of the world. They are very significant in the production of food supplies adequate for the growing human population. SEE ALSO Breeder; Breeding; Grains; Green Revolution; Photoperiodism.

John H. Perkins

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Boreal Forest *See Coniferous Forest.*

Botanical and Scientific Illustrator

The botanical or scientific illustrator creates accurate artworks under the close supervision of the scientist or author. Most works are made for publication in books or journals, but some may be for transparencies, charts, maps, diagrams, models, or murals. Curiosity, patience, and precision are required, as well as artistic creativity. This career could be ideal for people who enjoy spending hours looking for minute details on pressed **specimens** in a museum, or relish the idea of sketching live ones in the wild. Much sat-

specimen object or organism under consideration

An undated lithograph of Irish moss (right), creeping vine (center), ferns, figs, and other plants found in the American South.

isfaction can come from seeing publication of a drawing that is both beautiful and scientifically accurate.

The work of the botanical or scientific illustrator may be found in publications (particularly those dealing with plant taxonomy) and exhibitions of natural history museums, nature centers, and parks; and also in periodicals devoted to gardening, cooking, and health. Good artists accurately and artistically convey the author's ideas. Illustrators may have to decide how to show sections, magnifications, and various processes such as pollination or seed dispersal. A preliminary drawing could involve hours of comparing specimens and measurements under a microscope.

For persons interested in pursuing a career as a botanical or scientific illustrator, recommended courses at the high school level include basic design and drawing and science. Knowledge of Latin may be useful with scientific names; Spanish or Portuguese would be invaluable for work in the New World tropics. Computer graphics are opening additional career opportunities. The illustrator should also learn about printing techniques and will have to address issues of copyright and contracts.

Numerous universities and other institutions offer education in this field. Undergraduate degrees and master's degrees in botanical and scientific illustration are available. Various certificate programs, diplomas, courses, and internships are also offered at many institutions. The names of excellent private teachers, particularly in Great Britain, may be obtained from the Guild of Natural Science Illustrators (GNSI), American Society of Botanical Artists (ASBA), and Hunt Institute for Botanical Documentation.

A position might involve duties other than illustration, such as teaching, program and exhibition planning, collection curation, and writing. Many scientific illustrators work freelance, especially at first. The beginner may have to negotiate with a publisher before settling on a fee (a few hundred dollars in 1999) for a drawing. SEE ALSO HERBARIA; TAXONOMY.

James J. White

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Botanical Gardens and Arboreta

Botanical gardens and arboreta are living museums. Their collections are plants, and like any museum **specimens**, they are carefully identified, **accessioned**, labeled, and displayed for public enjoyment and education. They provide a rich opportunity for both the professional and interested public to learn more about the diverse world of plants, how to grow them, and the benefits they offer to society.

specimen object or organism under consideration

accessioned made a detailed record of an acquistion

People have been collecting and displaying plants for hundreds of years. During the sixteenth century the study and use of herbs for medicinal purposes motivated the founding of botanical gardens. The first were in Italy, at Pisa in 1543, and Padua and Florence in 1545. These gardens were initially associated with the medical schools of universities. Physic gardens, developed by professors of medicine who were the botanists of this period, served as both a teaching resource and a source of plants to make medicines. Interestingly, these original gardens are still in existence today. During the eighteenth and nineteenth centuries, the focus shifted towards taxonomy and the collection of specimens from around the world. Herbaria and libraries joined living collections as components of botanical gardens. Today, botanical gardens and arboreta are devoted mainly to plant culture and the display of ornamental plants and plant groups of special interest. Botanical exploration, taxonomy, and research can also be part of an individual garden's

A trellis with a cupola stands among the many flower beds on the 88-acre site of the Niagara Parks Botanical Garden in Ontario, Canada.

efforts. The latest estimates, derived from research for the International Union for Conservation of Nature and Natural Resources/World Wildlife Fund for Nature Botanic Gardens Conservation Strategy, indicate that there are approximately fourteen hundred botanical gardens and arboreta in the world. These may range in size from one or two acres to thousands of acres.

Botanical gardens and arboreta may be based on a design that gathers the trees, shrubs, and herbaceous plants in their respective taxonomic groups. Or, they may be grouped according to the region of the world where the plant grows in its native environment. Often, plants are used to create small, landscaped display gardens such as a rhododendron, wildflower, medicinal, or Japanese style garden, or examples of gardens for the home landscape.

In addition to their gardens and outdoor plant collections, botanical gardens and arboreta may include herbaria for the collection and preservation of dried plant specimens, libraries, research laboratories, production and display greenhouses, conservatories for the indoor display of tropical plants, educational classrooms, areas for interpretive exhibits, and public amenities such as a gift shop or restaurant.

Such diverse resources and facilities require a skilled staff of workers. The most important consideration in maintaining botanical gardens and arboreta is good plant-care practices. Horticulturists, trained in these practices, spend time on everything from lawn maintenance to systematic pruning of tree and shrub collections. Horticulturists are also responsible for collecting new plants, **propagating** seeds and cuttings, and maintaining accurate records of growth and health characteristics.

propagate to create more of through sexual or asexual reproduction

Other types of professional staff depend upon the objectives of the individual garden. They might include a plant pathologist or specialist in plant diseases, a landscape architect, research scientists, educators, librarian, and a membership and fund-raising specialist. A director is responsible for coordinating the entire botanic garden program.

Botanic gardens and arboreta may be independently established, part of a government agency, or connected to a college and university. Funding to support their activities may be derived through memberships, fees, tax support, or endowment funds, or a combination of these methods. SEE ALSO Curator of a Botanical Garden; Taxonomy.

Paul C. Spector

Botany

Botany is the study of plants. Plants make up a large fraction of all living organisms, and the study of botany is equally broad, including the **physiology**, genetics, anatomy, and **morphology** of plants, as well as their taxonomy, evolution, ecological relationships, and the many ways in which plants are used by people.

physiology the biochemical processes carried out by an organism

morphology shape and form

Like other scientific endeavors, the field of botany has grown immensely during the last decades of the twentieth century. It might also be said to have shrunk, however, as botanists have more carefully defined what a plant is. Fungi, algae, and photosynthetic bacteria, which were once classified as plants, are now placed in other kingdoms. Nonetheless, many who study these organisms still consider themselves botanists, and many university botany departments continue to include these organisms as topics of study within their departments.

Plants have an enormous influence on our lives through their use as foods, fibers, and fuels, as well as their critical role in recycling the gases of the atmosphere. More complete knowledge of botany improves our understanding of these influences, allowing us to use them more effectively, and more wisely. SEE ALSO Ecology, History of; Evolution of Plants, History of; Physiology, History of.

Richard Robinson

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Breeder

Plant breeding is the art and science of improving plant characteristics through the process of sexual reproduction. The goal of a plant breeder is to transfer genes from one plant to another and to select offspring that

A plant breeder performing research at the Volcani Institute in Israel.

have superior growth, yield, pest and disease resistance, or some other desirable trait.

To achieve this goal the breeder often begins the breeding process using primitive or wild forms of a particular plant species. Through a process of repeated sexual crossing and selection of improved forms, the breeder gradually reaches the goal. Often the hybridization process is lengthy, requiring time for the seed to grow into a mature flowering plant, which can then be compared to a **population** of seedlings from previous crosses. The newly selected plant is again sexually crossed with other improved plant types and gradually the desired trait or traits are incorporated into the new hybrid selection.

population a group of organisms of a single species that exist in the same region and interbreed

Plant breeders are trained in the science of genetics. Some receive a bachelor's degree in science, while others go on to earn a doctoral degree. This training is usually combined with a specialization in one or more types of crops such as grains, oilseeds, fruits, vegetable forage crops, or ornamental plants. A successful plant breeder must thoroughly understand the **physiology** and reproductive patterns and characteristics of the breeding materials.

physiology the biochemical processes carried out by an organism

Selecting for improved traits requires both the application of genetic principles as well as the ability to recognize sometimes small but very important changes in the plants when they are selected from one generation to the next during the breeding process. A well-trained plant breeder will also have knowledge of the "new genetics" of molecular biology and molecular genetics. Modern plant breeding combines the classical approach of sexual breeding with an understanding of gene structure. This knowledge allows the breeder to more rapidly combine desirable traits in the breeding population by establishing molecular genetic markers that can be associated with those traits.

Creativity is an important part of plant breeding. And developing a new plant that will increase the food supply or contribute to the beauty of the environment is quite rewarding. There are many career choices available to a plant breeder with training in molecular biology and classical breeding principles. One career path involves the application of genetic principles to plant improvement in a field or greenhouse. This is the role of the traditional breeder in the development of new plant varieties. There is a great need for individuals who possess these skills. Combining this role with training in molecular genetics increases the effectiveness of the breeder. Molecular genetics training also enables the breeder to work in a laboratory environment. Information developed in the laboratory can be transferred to breeders who use the information in a classical breeding program.

Typically, a plant breeder may teach and conduct research in a university or government laboratory. Many seed companies and biotechnology organizations employ plant breeders as well. Entry-level salaries in the 1990s ranged from $40,000 in an academic or government job to $60,000 to $80,000 in private industry. SEE ALSO Breeding; Genetic Engineer.

Roger H. Lawson

Breeding

The vast majority of the human population and most civilizations have depended on the productivity of plant-based agriculture for sustenance, vitality, and quality of life during the preceding five to fifteen millenia. During this time, and especially since the rediscovery of Gregor Mendel's principles of heredity in the late nineteenth century, the genetic content (genome) of crop plants has become a more important resource for crop management and production. The dynamic genomes of crop plants contain tens of thousands of genes that interact with themselves and the environment to determine the many traits affecting crop productivity. Gradually, humans have learned that the genomes of crop species and their relatives contain a range of genetic variation for many traits; how the genomes are transmitted from parent to progeny; a few of the myriad relationships among genomes, genes, the environment, and traits; some methods and mechanisms for maintaining or modifying the genomes; and how to select, capture, **propagate** and deliver the desirable genetic variation in forms suited to the agricultural systems and their societies. Much remains to be learned and understood.

propagate to create more of through sexual or asexual reproduction

Daniel Sarria, a Colombian corn breeder, inspects corn kernels on a light table.

holistic including all the parts or factors that relate to an object or idea

Plant breeding is the science ultimately concerned with the **holistic** and systematic creation of cultivars, cultivated varieties of plant species better suited to the needs and pleasures of human societies. In many ways, plant breeding is analogous to a large river system such as the Mississippi: it has a primary source (the gene pool of the plant species), a main river (the elite gene pool of plant breeding methods), tributaries (new technology and scientific disciplines), the ability to adapt to the prevailing conditions and forces of nature, and it is replenished by recycled water (germplasm, all genotypes of a species). Plant breeders devise and deploy methods that, in accordance with their resources, the nature of the plant and production environment, and the prevailing goals of society, integrate information and material from the tributaries to produce better cultivars. The scientific tributaries have included the biological (e.g., genetics, botany, biochemistry, plant pathology, entomology), physical (e.g., mathematics, chemistry, computer), and analytical (e.g., experimental design and statistics) sciences. Some important technological tributaries include methods for storing seed or other propagules, the computer for data analysis and management, and tools or machines for conducting the many experiments and evaluating the progeny needed to create a superior cultivar. New tributaries include genomics, molecular biology, and genetic engineering. While the tributaries have varied with the nature of the crop species and the resources and goals of the societies they support, the primary roles of the plant breeder—integration, evaluation, and selection—have been constant.

Components and Challenges of Plant Breeding Programs

Plant breeding programs consist of several steps that are usually conducted as reiterative procedures:

1. hire talented and cooperative scientists (e.g., plant breeder, scientists in other disciplines, and technical staff)
2. understand the ecology of the plant, the target environment, the system of crop production, and the consumers

3. define the target environment for crop production (e.g., Where and how are the crops grown? What is the prevailing ecology therein?)
4. assemble and maintain the necessary physical resources
5. identify clear goals for selection regarding the type of cultivar, the traits, and their expression
6. select or create testing environments representative of the target environment
7. survey and choose germplasm to serve as parents and sources of genes (the crop and other species, cultivars, accessions [individual samples of seed] from germplasm reserves, and genes)
8. identify and create genetic variation among the parents and their progeny by evaluating the parents, mating the parents, and evaluating their progeny and occasionally by modifying the parents' genome or introducing genes through genetic engineering and transformation
9. evaluate and select the progeny that optimize production in the target environment.

When practiced on a continuous basis, these steps have achieved impressive results for several species and target environments.

Plant breeding programs negotiate numerous challenges along the path of improvement. The reproductive biology and growth habit of the plant are primary factors that dictate breeding methods, their implementation, progress from selection, and the type of cultivar (e.g., **hybrid**, pure line, clonal, **population**, or other). Some important considerations include the mode of reproduction (sexual, vegetative, or both), flower structure (perfect or imperfect), prevailing type of pollination (e.g., autogamous [self] or allogamous [other], wind, or insect), and methods to induce flowering, make controlled matings between the selected parents, and produce an adequate supply of progeny for evaluation and distribution. Considerations of the growth habit would include the length of the juvenile period (especially with trees) and if the species has an annual or perennial habit in the target environment.

hybrid a mix of two species

population a group of organisms of a single species that exist in the same region and interbreed

The organization of the plant's genome also affects breeding strategy and the rate of progress. The plant genome is partitioned into the nucleus, mitochondrion (mt), and plastid (pt; e.g., chloroplast). The mt and pt genomes contain relatively few genes (hundreds) and in most **angiosperm** species are transmitted to the progeny exclusively through the cytoplasm of the female gametes (the egg cell in the embryo sac). The maternal inheritance of those genomes may dictate which parents are used as males and females. Plant nuclear genomes contain tens of thousands of genes as parts of several independent chromosomes, are inherited biparentally through the male (sperm nuclei in the generative cell of the pollen grain) and female gametes, and often contain more than two complete sets of chromosomes (polypoidy). For example, maize (*Zea mays* L.) and rice (*Oryza sativa* L.) are **diploid** because the nuclei of their somatic cells contain two complete sets of chromosomes, one each from the maternal and paternal parents. In contrast, cultivated alflalfa (*Medicago sativa* L.) and bread wheat (*Triticum aestivum* L.) are autotetraploid and allohexaploid because their somatic cells

angiosperm a flowering plant

diploid having two sets of chromosomes, versus having one (haploid)

progenitor parent or ancestor

polyploidy having multiple sets of chromosomes

contain four (from the same species) and six (from three different **progenitor** species) complete sets of chromosomes, respectively. **Polyploidy** challenges breeders because it leads to more complex inheritance patterns and may hinder identification of desirable progeny in segregating populations.

The ecology of the target environment and the plant affect the evaluation and selection of parents and progeny in myriad ways (e.g., climate, soil, organic diversity, and the subsequent stress on crop production). The relative merit of the germplasm (e.g., parent, progeny, or cultivar) may vary greatly and depend upon certain elements of the environment (i.e., genotype and environment interaction, GxE). For example, a disease-resistant cultivar may have superior productivity when evaluated in a disease-laden environment but the same cultivar may be inferior when tested in a disease-free environment. GxE is a major challenge for every plant-breeding program because so many factors could influence the plant's growth and productivity during its life cycle. GxE is managed by testing germplasm in samples of relatively few environments and treatments intended to resemble the prevailing conditions of the target environment. Inadequate testing may result in a poor choice of genotypes, less genetic progress, and, sometimes, truly inferior cultivars.

Accomplishments of Plant Breeding Programs: Some Examples

domesticate to tame an organism to live with and to be of use to humans

Plant breeders have achieved some significant genetic modifications of plant species. Crop **domestication**, although unrecorded for most plants, provided the critical foundation for subsequent cycles of distribution, adaptation, mating, and selection. Some products of those cycles include rice and wheat of short stature and increased yield, beets (*Beta vulgaris* L.) with increased sucrose concentration, *Brassica napus* L.with edible oil, the forms of *Brassica oleracea* L. (e.g., cauliflower, cabbage, kale, broccoli, kohlrabi, and brussels sprouts), and high-yielding maize (corn). The achievements with rice and wheat (the Green Revolution) significantly enhanced food production for billions of persons and were partially recognized in 1970 when Norman Borlaug received a Nobel Prize for his role in developing and promoting new cultivars of wheat.

In the United States maize is an example of a crop that has been quickly and significantly modified through plant breeding. Maize is a tropical grass domesticated by central American natives, possibly from the wild relative teosinte (*Zea mexicana*). It was cultivated throughout the Americas before the colonization by Europeans, who adopted and expanded maize production. In the 1920s breeding methods changed dramatically: inbred lines (parents) were developed through generations of self-pollination and selection; the inbred lines were mated in specific combinations; many combinations were tested; a few combinations exhibited exceptional vigor and productivity; and the seed produced from selected matings was grown as the crop (i.e., the F1 or hybrid generation of the mating between the inbred lines). Previously, breeding methods in the United States emphasized selection of seed and individual plants produced through random, uncontrolled matings within locally adapted varieties and such open-pollinated seed was grown as the crop. In the 1930s farmers quickly substituted hybrid cultivars for the open-pollinated cultivars because the hybrids had higher and more consistent yield. Concomitantly, management practices changed. The average grain yield of maize increased from 30 to 120 bushels per acre from the 1930s to the 1990s. About 50 percent of the increase is due to genetic changes mediated by breeding for higher yield of grain, resistance to **biotic** and **abiotic** stress, and the ability to respond to more intensive management (e.g., increased application of fertilizer and seeding rates).

biotic involving or related to life

abiotic nonliving

Plant Breeding Programs and Germplasm Reserves. The target environment and societies' goals sometimes change in dynamic and unpredictable ways that render existing cultivars obsolete. Cultivars with improved adaptation may be bred if genetic variation (i.e., genes and combinations thereof) exists for the traits of interest. To manage this uncertainty, germplasm reserves or gene banks have been established worldwide with the primary goals of collecting and maintaining the broadest possible array of genetic variation for economically important plant species. In the United States a network of Plant Introduction Stations are financed by the federal and state governments to provide this service. The reserves are important because:

- the gene pool of existing cultivars represents only a subsample of the genetic variation for a given species
- favorable genes are certainly contained in other gene pools
- human activity has reduced the native gene pools of most crop species and their wild relatives in agricultural and natural settings
- the reserves have provided useful genes
- methods for investigating gene pools have been crude but there are good prospects for improvement
- our ability to engineer genes and complete organisms to meet the demands of crop production is woefully inadequate and will need all the help provided by nature. SEE ALSO Breeder; Cultivar; Genetic Engineering; Green Revolution; Hybrids and Hybridization; Polyploidy; Propagation; Reproduction, Sexual; Seeds.

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Breeding Systems

Breeding systems in plants refer to the variety of ways plants answer the general question of "Who mates with whom" by answering specific questions such as whether flowers mature at the same time, whether a plant has more than one kind of flower or differs from other plants in types of flow-

Wind blows pollen off the male cone of a pine tree.

ers, and whether there are chemicals that keep certain plants from mating with each other.

Outcrossing and Inbreeding

Most vertebrate species consist of separate male and female individuals. In contrast, the majority of flowering plants are hermaphroditic, with both pollen and ovules produced by the same plant. As a consequence, many flowering plants are capable of self-fertilization (selfing), with seeds resulting from pollen and eggs produced by the same plant. The self pollen that fertilizes the egg may be produced by the same flower (called autogamy) or by different flowers on the same plant (geitonogamy). Selfing or mating among close relatives (inbreeding) often results in offspring that have reduced vigor and produce fewer offspring compared to offspring from matings between unrelated plants (outcrossing). This reduction in fitness of selfed offspring relative to outcrossed offspring is referred to as inbreeding depression. If both selfing levels and levels of inbreeding depression are high, natural selection may favor mechanisms that promote outcrossing. High levels of inbreeding depression are likely to be found in populations that have been outcrossing for a long time. In contrast, in populations that have been inbreeding (high selfing rates) for many generations, inbreeding depression levels may now be low because harmful genes have already been eliminated from the population by natural selection.

Selfing may also have direct advantages. Selfing plants may have an *automatic selection advantage* and contribute more genes to the next generation because they contribute both maternal genes (through the egg) and paternal genes (through pollen) to selfed seeds, and they also contribute pollen (and thus paternal genes) to other plants, spreading their genes further. In contrast, outcrossing plants contribute pollen to other plants, but only maternal genes to their own seeds. This automatic selection advantage will lead to selection for selfing if selfing does not decrease outcrossing (thereby limiting the spread of genes), and if inbreeding depression is not too severe. In addition, selfing tends to produce offspring more similar to the parent plant than outcrossing. If seeds are dispersed locally into habitat similar to that of the parent, these selfed offspring may do better than outcrossed offspring. In habitats where pollen is limited because of low population density or because there are few pollinators, selfing may also provide *reproductive assurance* with a guaranteed source of pollen. Some plants, such as touch-me-not (*Impatiens*) and some violet species (*Viola*) have evolved flowers that are pollinated autogamously and never open (called cleistogamy), as well as the more showy open flowers (chasmogamy).

Heterostyly

Several factors may promote outcrossing, including separation of male and female function in time or space. In **heterostylous** plants such as the primrose (*Primula*) described by English naturalist Charles Darwin (1809–1882), there are two floral forms (distyly). In one form, pin flowers have long styles and short stamens. Thrum flowers have short styles and long stamens. This positioning favors outcrossing with transfer of pollen between the pin and thrum plants by pollinators.

heterostylous having styles (female flower parts) of different lengths, to aid cross-pollination

Dichogamy

In dichogamy, pollen is released and the stigma is receptive (ready to receive pollen) at different times. There are two types: in protandry ("early male"), the pollen is shed before the stigmas are receptive, while in protogyny ("early female"), the stigmas are receptive before the pollen is shed. Even greater outcrossing is promoted by synchronizing all of the flowers on the plant for the same sex, so that all stigmas are receptive together, either before or after all pollen is shed.

Dioecy

Spatial separation of the sexes onto different flowers or different plants may also promote outcrossing. An individual flower may have only stamens (male) or only **pistils** (female), or both (hermaphroditic) in the same flower, and plants and populations may have various combinations of flowers. Monoecious ("one house") populations have both sexes of unisexual flowers on each plant (e.g., corn has tassels of male flowers and an ear of female flowers on the same plant). Gynodioecious populations, consisting of female and hermaphroditic plants, are also possible. Dioecious ("two-house") populations consist of male-only and female-only plants (e.g., marijuana, or *Cannabis*). Dioecy has arisen independently in the flowering plants many times. About 6 percent of flowering plant species are dioecious, and the incidence of dioecy is particularly high in the Hawaiian Islands (14.7 percent) and in New Zealand (12 to 13 percent). Flowering plants also have more complicated patterns of sex expression, and some plants are even capable of switching sex through time.

pistil the female reproduction organ

Two major theories have been proposed to explain the evolution of dioecy. One theory suggests that dioecy has evolved as a mechanism to avoid inbreeding depression and enforce outcrossing between unisexual plants. The other theory suggests that patterns of resource allocation between male and female function (sex allocation) are critical. According to this theory, dioecy should evolve from hermaphroditism when greater investment of resources in flowers of one sex yields a disproportionate gain in reproductive success. In such cases, it would be advantageous to separate the sexes to allow more efficient resource allocation.

Self-incompatibility

gametophyte the haploid organism in the life cycle

Even without spatial or temporal (time-related) separation, chemical incompatibility between the stigma or style and pollen of the same plant can also promote outcrossing. Molecular data suggest that self-compatibility is the ancestral condition in flowering plants and that self-incompatibility has evolved independently many times. In plants such as tobacco (*Nicotiana*) that have **gametophytic** self-incompatibility (GSI), pollen tubes germinate but fail to grow through the style if they are chemically incompatible. In GSI, the incompatibility reaction is determined by the combination of the self-incompatibility (SI) genes of the maternal plant and the SI genes of the pollen grain. GSI is found in several species, including tobacco and some grasses.

In sporophytic self-incompatibility (SSI), the incompatibility reaction is controlled by the combination of maternal plant SI genes in the stigma and the SI genes of the plant that produced the pollen, rather than those of the pollen grain itself. Incompatible reactions cause the pollen tube to stop growing on or near the stigma. Multi-allelic SSI systems have many incompatibility types, and proteins that cause the incompatibility reaction are produced by the anthers and are present in the outer layer of the pollen grain. Broccoli and many other members of the mustard family (Brassicaceae) have multi-allelic SSI.

In contrast, many plants with SSI have only two or three incompatibility types, but are heterostylous (e.g., shamrock [*Oxalis*], and water hyacinth [*Eichhornia*], a noxious, invasive aquatic weed). SEE ALSO Flowers; Pollination Biology; Reproduction, Asexual; Reproduction, Fertilization and; Reproduction, Sexual; Seed Dispersal.

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Britton, Nathaniel

American Botanist
1859–1934

Nathaniel Lord Britton was an American botanist who helped found the New York Botanical Garden and build it into a premier research institution. Britton was born in 1859 in Staten Island, New York, and received both his undergraduate and graduate degrees in geology and mining engineering from Columbia University. His professional interest in botany began while he was working for the New Jersey Geologic Survey, during which time he prepared a list of plants found in the state. He became a professor at Columbia, first in geology and later in botany. In 1885 he married Elizabeth Knight, one of the foremost **bryologists** in the country.

bryologist someone who studies bryophytes, a division of nonflowering plants

Britton and his wife were inspired by a visit to the Royal Botanic Gardens at Kew, England, and returned in 1891 to the United States to begin planning for what would become the New York Botanical Garden. Britton was its first director, a post he held until his retirement in 1929. Through his administrative skill, scholarship, energy, and force of personality, Britton built the garden into a world-class center for research in plant taxonomy, and the finest botanical garden in the country.

Britton was a prolific author, writing hundreds of scientific papers and several important books. He was the principal author of the *Illustrated Flora* of the northeastern United States, a text that was at one time the major guide to the plants of this region. He published many papers on the flora of the West Indies, and was coauthor of *The Cactaceae of the World.* A large number of **genera** of flowering plants bear his name, as does *Brittonia*, a major journal of American plant taxonomy published by the New York Botanical Garden.

genera plural of genus

Britton undertook a major revision of the nomenclature of the plants of North America, creating the American Code of Botanical Nomenclature in 1892. Britton meant this system to replace the International Code used widely at that time. Although most major research institutions did not adopt his system, the U.S. Department of Agriculture did, assuring it a prolonged life, if not widespread use. The American Code, however, fell further and further out of favor after Britton's death in 1934, and is no longer used today. SEE ALSO Botanical Gardens and Arboreta; Curator of a Botanical Garden; Taxonomist; Taxonomy; Taxonomy, History of.

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Brongniart, Adolphe

French Paleobotanist
1801–1876

Adolphe Brongniart is considered to be the founder of French paleobotany (the study of fossil plants), but his influence and that of his family extends far beyond the borders of France. Born 1801 in Sèvres, France, where his father ran a porcelain factory, Adolphe came from a very well-known family. His grandfather, Alexandre-Théodore Brongniart, was a respected architect who designed the Bourse (the Paris Stock Exchange); his father, Alexandre Brongniart (1770–1847), and Georges Cuvier (1769–1832) are considered the fathers of **stratigraphic geology**. They developed geologic mapping on a scale that could be both interpretive and predictive, and were pioneers in using fossils to determine the age of rocks.

stratigraphic geology the study of rock layers

Adolphe greatly benefited from his father's wide-ranging interests. Before he was twenty, they had traveled together to many areas of the continent, including western France, the Jura Mountains, Switzerland, and Italy. In 1824 and 1825 they visited Scandinavia and the British Isles. These trips focused on botany, geology, or both, so that Adolphe was exposed to fossil plants from a variety of places while still relatively young, giving him a more global view of fossil floras than many scientists of his day.

In 1822 Adolphe Brongniart published his initial classification of all fossil plants then known, a system that was also adopted for the living plants in the Museum of Natural History in Paris. In 1828 he published the first of two volumes of a more complete description of the fossil plants of the world, *Histoire des Végétaux Fossiles.* At the age of twenty-five, he received a doctor of medicine degree with a thesis on the living plant family Rhamnaceae (the buckthorn family). He was already known for his research on fossil plants at this time. In 1831 he was appointed as a naturalist aide at the museum and two years later became a professor of botany there. More than any other interest, paleobotany occupied him until he died.

silicified composed of silicate minerals

Although Brongniart published numerous works on compression fossils (thin, carbonaceous films on the rock surface), he is equally well known for his studies of internal anatomy in ancient plants. One of his first papers on this subject was on Carboniferous ferns and was published in 1837. Brongniart used comparative anatomy of fossil and living plants to better understand the classification of the fossils and was clearly a pioneer in the area of using thin sections to study the internal structure of fossil plants. His study of the structure of **silicified** Carboniferous seeds, *Recherches sur les Graines silicifiées du Terrain houiller de St.-Etienne* (1881), has been called a model of comparative anatomy of fossil plants. Unfinished at his death in 1876, the book was published posthumously.

Adolphe Brongniart was the first to publish a classification of all known fossil plants and pioneered the use of comparative anatomy in the study of plant fossils. Because of his broad knowledge of fossil plants from many regions, he was able to recognize a distinct succession of floras through time and regularly correlated fossils with particular rocks (biostratigraphy). Finally, Brongniart was probably the first to spend his life working in paleobotany as a primary pursuit and not just as a sideline to medicine or business, making him the first professional paleobotanist in history. SEE ALSO Evolution of Plants; Evolution of Plants, History of; Taxonomy.

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Bryophytes

vascular related to transport of nutrients

epiphytes plants that grow on other plants

Plant scientists recognize two kinds of land plants: bryophytes (nonvascular land plants) and tracheophytes (**vascular** land plants). Bryophytes are small, herbaceous plants that grow closely packed together in mats or cushions on rocks or soil or as **epiphytes** on the trunks and leaves of forest trees.

Bryophytes are distinguished from tracheophytes by two important characteristics. First, in all bryophytes the ecologically persistent, photosynthetic phase of the life cycle is the **haploid**, **gametophyte** generation rather than the **diploid sporophyte**; bryophyte sporophytes are very short-lived, are attached to and nutritionally dependent on their gametophytes, and consist of only an unbranched stalk, or seta, and a single, terminal sporangium. Second, bryophytes never form xylem tissue, the special lignin-containing, water-conducting tissue that is found in the sporophytes of all vascular plants. At one time, all bryophytes were placed in a single phylum, intermediate in position between algae and vascular plants. Modern studies of cell **ultrastructure** and molecular biology, however, confirm that bryophytes comprise three separate evolutionary **lineages**, today recognized as mosses (phylum Bryophyta), liverworts (phylum Marchantiophyta), and hornworts (phylum Anthocerotophyta). Following a detailed analysis of land plant relationships, Paul Kenrick and Peter R. Crane proposed that the three groups of bryophytes represent a structural level in plant evolution, identified by their monosporangiate life cycle. Within the bryophytes, liverworts are the geologically oldest group, sharing a fossil record with the oldest vascular plants (Rhyniophytes) in the Devonian era.

haploid having one set of chromosomes, versus having two (diploid)

gametophyte the haploid organism in the life cycle

diploid having two sets of chromosomes, versus having one (haploid)

sporophyte the diploid, spore-producing individual in the plant life cycle

ultrastructural the level of structure visible with the electron microscope; very small details of structure

lineage ancestry; the line of evolutionary descent of an organism

Mosses

Of the three phyla of bryophytes, greatest species diversity is found in the mosses, with up to fifteen thousand species recognized. A moss begins its life cycle when haploid spores, which are produced in the sporophyte capsule, land on a moist **substrate** and begin to germinate. From the one-celled spore a highly branched system of **filaments**, called the protonema, develops. Cell specialization occurs within the protonema to form a horizontal system of reddish-brown anchoring filaments and upright green filaments. Each protonema, which superficially resembles a **filamentous** alga, can spread over several centimeters to form a fuzzy green film over its substrate. As the protonema grows, some cells of the specialized green filaments form leafy buds that will ultimately form the adult gametophyte shoots. Numerous shoots typically develop from each protonema so that, in fact, a single spore can give rise to a whole clump of moss plants. Each leafy shoot continues to grow **apically**, producing leaves in spiral arrangement on an elongating stem. In many mosses the stem is differentiated into a central strand of thin-walled water-conducting cells, called hydroids, surrounded by a **parenchymatous** cortex and a thick-walled epidermis. The leaves taper from a broad base to a pointed apex and have lamina that are only one-cell-layer thick. A hydroid-containing midvein often extends from the stem into the leaf. Near the base of the shoot, reddish-brown multicellular rhizoids emerge from the stem to anchor the moss to its substrate. Water and mineral nutrients required for the moss to grow are absorbed, not by the rhizoids, but rather by the thin leaves of the plant as rain water washes through the moss cushion.

substrate the physical structure to which an organism attaches

filament a threadlike extension

filamentous thin and long

apically at the tip

parenchyma thin-walled cells of various sizes

As is typical of bryophytes, mosses produce large, multicellular sex organs for reproduction. Many bryophytes are unisexual, or sexually **dioicous**. In mosses male sex organs, called antheridia, are produced in clusters at the tips of shoots or branches on the male plants; female sex organs, the archegonia, are produced in similar fashion on female plants. Numerous motile sperm are produced by **mitosis** inside the brightly colored, club-shaped an-

dioicous having male and female sexual parts on different plants

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

DISTINGUISHING CHARACTERISTICS OF MOSSES, LIVERWORTS, AND HORNWORTS

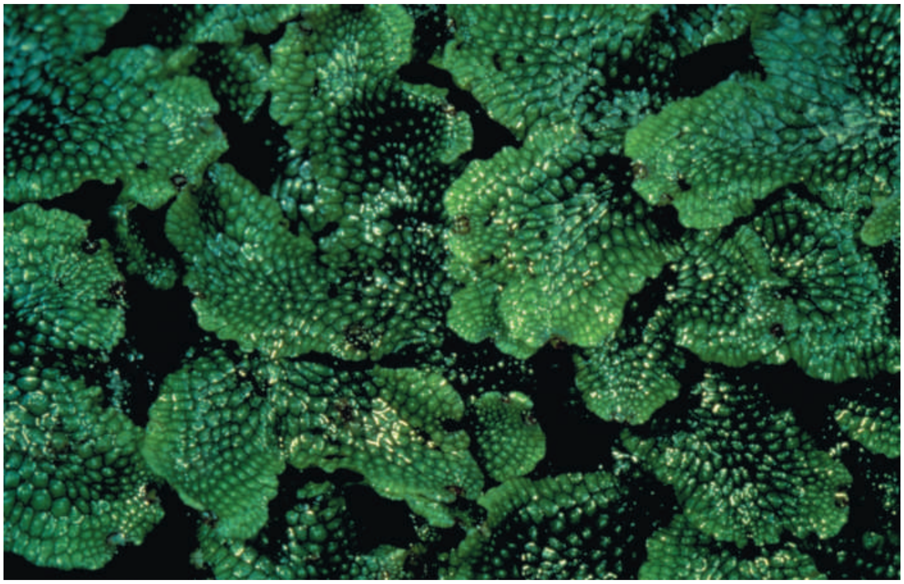
Characteristics	Mosses (Bryophyta)	Liverworts (Marchantiophyta)	Hornworts (Anthocerotophyta)
Protonema	Filamentous, forming many buds	Globose, forming one bud	Globose, forming one bud
Gametophyte form	Leafy shoot	Leafy shoot or thallus; thallus simple or with air chambers	Simple thallus
Leaf arrangement	Leaves in spirals	Leaves in three rows	Not Applicable
Leaf form	Leaves undivided, midvein present	Leaves divided into two-plus lobes, no midvein	Not Applicable
Special organelles	None	Oil bodies	Single plastids with pyrenoids
Water-conducting cells	Present in both gametophyte and sporophyte	Present only in a few simple thalloid forms	Absent
Rhizoids	Brown, multicellular	Hyaline, one-celled	Hyaline, one-celled
Gametangial position	Apical clusters (leafy forms)	Apical clusters (leafy forms) or on upper surface of thallus	Sunken in thallus, scattered
Stomates	Present on sporophyte capsule	Absent in both generations	Present in both sporophyte and gametophyte
Seta	Photosynthetic, emergent from gametophyte early in development	Hyaline, elongating just prior to spore release	Absent
Capsule	Complex with operculum, theca, and neck; of fixed size	Undifferentiated, spherical, or elongate; of fixed size	Undifferentiated, horn-shaped; growing continuously from a basal meristem
Sterile cells in capsule	Columella	Spirally thickened elaters	Columella and pseudoelaters
Capsule dehiscence	At operculum and peristome teeth	Into four valves	Into two valves

theridia while a single egg develops in the base of each vase-shaped archegonium. As the sperm mature, the antheridium swells and bursts open. Drops of rainwater falling into the cluster of open antheridia splash the sperm to nearby females. Beating their two whiplash **flagellae**, the sperm are able to move short distances in the water film that covers the plants to the open necks of the archegonia. Slimy mucilage secretions in the archegonial neck help pull the sperm downward to the egg. The closely packed arrangement of the individual moss plants greatly facilitates fertilization. Rain forest bryophytes that hang in long festoons from the trees rely on torrential winds with the rain to transport their sperm from tree to tree, while the small pygmy mosses of exposed, **ephemeral** habitats depend on the drops of morning dew to move their sperm. Regardless of where they grow, all bryophytes require water for sperm dispersal and subsequent fertilization.

flagellae threadlike extensions of the cell membrane, used for movement

ephemeral short-lived

Embryonic growth of the sporophyte begins within the archegonium soon after fertilization. At its base, or foot, the growing embryo forms a nutrient transfer zone, or placenta, with the gametophyte. Both organic nutrients and water move from the gametophyte into the sporophyte as it continues to grow. In mosses the sporophyte stalk, or seta, tears the archegonial enclosure early in development, leaving only the foot and the very base of the seta embedded in the gametophyte. The upper part of the archegonium remains over the tip of the sporophyte as a caplike calyptra. Sporophyte growth ends with the formation of a sporangium (the capsule) at the tip of the seta. Within the capsule, water-resistant haploid spores are formed by meiosis. As the mature capsule swells, the calyptra falls away. This allows the capsule to dry and break open at its tip when the spores are mature. Special membranous structures, called peristome teeth, that are folded down into the spore mass now bend outward, flinging the spores into the drying



The bryophyte common liverwort (*Marchantia polymorpha*).

winds. Moss spores can travel great distances on the winds, even moving between continents on the jet streams. Their walls are highly protective, allowing some spores to remain **viable** for up to forty years. Of course, if the spore lands in a suitable, moist habitat, germination will begin the cycle all over again.

viable able to live or to function

Liverworts and Hornworts

Liverworts and hornworts are like mosses in the fundamental features of their life cycle, but differ greatly in organization of their mature gametophytes and sporophytes. Liverwort gametophytes can be either leafy shoots or flattened **thalli**. In the leafy forms the leaves are arranged on the stem in one ventral and two **lateral** rows or ranks, rather than in spirals like the mosses. The leaves are one cell-layer thick throughout, never have a midvein, and are usually divided into two or more parts called lobes. The ventral leaves, which actually lie against the substrate (soil or other support), are usually much smaller than the lateral leaves and are hidden by the stem. Anchoring rhizoids, which arise near the ventral leaves, are colorless and unicellular. The flattened ribbonlike to leaflike thallus of the thallose liverworts can be either simple or structurally differentiated into a system of dorsal air chambers and ventral storage tissues. In the latter type the dorsal epidermis of the thallus is punctuated with scattered pores that open into the air chambers. Liverworts synthesize a vast array of volatile oils, which they store in unique **organelles** called oil bodies. These **compounds** impart an often spicy aroma to the plants and seem to discourage animals from feeding on them. Many of these compounds have potential as antimicrobial or anticancer pharmaceuticals.

thallus simple, flattened, nonleafy plant body

lateral away from the center

organelle a membrane-bound structure within a cell

compound a substance formed from two or more elements

Liverworts. Liverwort sporophytes develop completely enclosed within gametophyte tissues until their capsules are ready to open. The seta, which is initially very short, consists of small, thin-walled hyaline cells. Just prior to capsule opening, the seta cells lengthen, thereby increasing the length of the seta up to twenty times its original dimensions. This rapid elongation pushes the darkly pigmented capsule and upper part of the whitish seta out of the gametophytic tissues. With drying, the capsule opens by splitting into four segments, or valves. The spores are dispersed into the winds by the twisting motions of numerous intermixed **sterile** cells called elaters. In contrast to mosses, which disperse their spores over several days, liverworts disperse the entire spore mass of a single capsule in just a few minutes.

sterile not capable or involved in reproduction

Hornworts. Hornworts resemble some liverworts in having simple, unspecialized thalloid gametophytes, but they differ in many other characters. For example, colonies of the **symbiotic cyanobacterium** *Nostoc* fill small cavities that are scattered throughout the ventral part of the hornwort thallus. When the thallus is viewed from above, these colonies appear as scattered blue-green dots. The cyanobacterium converts nitrogen gas from the air into ammonium, which the hornwort requires in its metabolism, and the hornwort secretes carbohydrate-containing mucilage, which supports the growth of the cyanobacterium. Hornworts also differ from all other land plants in having only one large, algal-like **chloroplast** in each thallus cell. Hornworts get their name from their long, horn-shaped sporophytes. As in other bryophytes, the sporophyte is anchored in the gametophyte by a foot through which nutrient transfer from gametophyte to sporophyte occurs. The rest of the sporophyte, however, is actually an elongate sporangium in which meiosis and spore development take place. At the base of the sporangium, just above the foot, is a mitotically active **meristem**, which adds new cells to the spore-producing zone throughout the life span of the sporophyte. In fact, the sporangium can be releasing spores at its apex at the same time that new spores are being produced by meiosis at its base. Spore release in hornworts takes place gradually over a long period of time, and the spores are mostly dispersed by water movements rather than by wind.

symbiosis a relationship between two organisms from which each derives benefit

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

chloroplast the photosynthetic organelle of plants and algae

meristem the growing tip of a plant

Mosses, liverworts, and hornworts are found throughout the world in a variety of habitats. They flourish particularly well in moist, humid forests like the fog forests of the Pacific Northwest or the **montane** rain forests of the Southern Hemisphere. Their ecological roles are many. They provide seed beds for the larger plants of the **community**, they capture and recycle nutrients that are washed with rainwater from the canopy, and they bind the soil to keep it from eroding. In the Northern Hemisphere peatlands, wetlands often dominated by the moss *Sphagnum*, are particularly important bryophyte communities. This moss has exceptional water-holding capacity, and when dried and compressed forms a coal-like fuel. Throughout northern Europe, Asia, and North America, peat has been harvested for centuries for both fuel consumption and horticultural uses, and today peat lands are managed as a sustainable resource. SEE ALSO EVOLUTION OF PLANTS; GAMETOPHYTE; NITROGEN FIXATION; PEAT BOGS; REPRODUCTION, ALTERNATION OF GENERATIONS AND; SPOROPHYTE.

montane growing in a mountainous region

community a group of organisms of different species living in a region

Barbara Crandall-Stotler

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Burbank, Luther

American Horticulturist
1849–1926

Luther Burbank was the most well-known plant breeder of the Age of Agriculture. He was born March 7, 1849, in Lancaster, Massachusetts. He had little formal science training, but his efforts to better the human condition by improving useful plants made him a folk hero throughout the world. Burbank's work is said to have advanced the science of horticulture by several decades.

Luther Burbank.

sterile not capable or involved in reproduction

cultivation growth of crop plants, or turning the soil for this purpose

nurseryman a worker in a plant nursery

Burbank's first, and foremost, contribution is evidenced with every baked potato and french fry eaten today. At the age of twenty-four, Burbank discovered a seed ball on the normally **sterile** Early Rose potato. Inspired by English naturalist Charles Darwin's *The Variation of Animals and Plants Under Domestication*, Burbank cultivated these seeds and used them to "build" the first white potato, the basis for the modern Burbank Russet Idaho potatoes.

In 1875, with $150 in proceeds from the sale of most of his potato stock, Burbank journeyed by train to California in search of a suitable climate for year-round **cultivation**. Burbank saw greater potential in the soil and climate of the state than in its famed gold mines. After a few rough years, Burbank was able to establish himself in Santa Rosa as a **nurseryman** who tried, and usually delivered, the impossible. After fulfilling an order for twenty thousand bearing prune trees from seed in nine months, Burbank earned a reputation as one who could succeed where others feared to try.

In 1893 Burbank's "New Creations in Fruits and Flowers" catalog created an international sensation, causing some to object that Burbank claimed powers of creation reserved only for God. Burbank believed that his plants were inventions that were developed in concert with God's agent: nature.

At his nursery, greenhouses, and experimental gardens, Burbank specialized in horticultural novelties, working on an at-demand basis for nurserymen. At any one time, Burbank might have tens of thousands of plants in cultivation and hundreds (perhaps thousands) of experiments in progress.

Burbank worked with flowers, fruits, trees, cacti, grasses, grains, and vegetables. His long-running experiments and his keen awareness of the correlation of nascent plant features with desirable traits in mature plants, helped him introduce or develop more than eight hundred varieties throughout his fifty-year career—that's a new plant every twenty-three days.

Among the many varieties he developed several are still widely used today: the Paradox Walnut (*Juglans Regina x J. Californica var.*), developed as a fast-growing hardwood tree for the furniture industry, today the most com-

complex hybrid hybridized plant with more than two parent plants

quadruple hybrid hybridized plant with four parents

mon rootstock for walnuts; the 1906, Santa Rosa plum, a **complex hybrid,** still among the most cultivated varieties in the United States; and the **quadruple hybrid** Shasta daisy (*Chrysanthemum leucanthemum hybridum*), introduced in 1901, one of the most popular flowers in cutting gardens today.

Some of Burbank's more unusual novelties include: more than thirty-five varieties of spineless cacti for improved fruit and better forage for livestock; the plumcot, the first creation of an entirely new stone fruit; and the white blackberry, a flavorful berry without pigment to stain hands and clothing.

Burbank's methods were not unique, but he applied them on a greater scale than previously known. A wider range of experimental varieties, a longer period of study, and a greater number of experiments underway at a given time gave Burbank an unmatched breadth of experience and genetic variability from which to work. Using space- and time-saving methods such as grafting (sometimes hundreds of varieties on one nurse tree) and budding allowed him to grow several million plants during his career.

Burbank imposed environmental changes and numerous cross-fertilizations on imported plants from across the globe to induce as many perturbations or variants as possible. From the most promising plants Burbank continued to select, hybridize, reselect, and rehybridize for several generations until he developed a marketable plant.

He employed all of his senses to judge the worthiness of his creations. His criteria for success included both attractiveness and utility. "The urge to beauty," according to Burbank, "is as important as the urge to bread." (Explanation: Beauty is as fundamental as bread.)

Although Burbank had little formal scientific training in his early years, he enjoyed the friendship and support of many leading scientists. Favorable impressions of his work led to a prestigious and lucrative five-year Carnegie Foundation grant. His brand of applied scientific practice and the increasingly astounding accounts of his new creations, however, provoked scientists' ire as well as imagination.

Burbank believed heredity and environmental circumstances governed a plant's "life force." He asserted, as did French naturalist Jean-Baptiste Lamarck (1744–1829), that acquired characteristics (accrued forces) were inheritable, a position that became increasingly unacceptable in the scientific world. He felt that many of the mutations heralded by ever more popular Mendalians were simply hybrids.

As his career progressed, Burbank became as well known for his unorthodox social and religious beliefs as for his plant developments. In 1907 he wrote a book entitled *The Training of the Human Plant* that advocated that children should learn from natural surroundings until the age of ten, foregoing formal schooling. Burbank stated publicly that he felt himself to have supernatural powers.

Just before his death in 1926, Burbank was quoted in an article as proclaiming himself an "infidel," like Christ, a man who did not believe in traditional religion. This caused a firestorm of debate across the country. Burbank later clarified his meaning on national radio, "I am a lover of man and of Christ as a man and his work, and all things that help humanity. . . . I prefer and claim the right to worship the infinite, everlasting, almighty God of this vast universe as revealed to us gradually, step by step, by the demonstrable truths of our savior, science."

Burbank groomed no successors to his work. Although Burbank kept copious notes, he did not have the protection of plant patent laws, and he was protective of his practices. His efforts to institute such laws eventually encouraged their passage, but not until after his death. For years, despite his secretiveness, Burbank allowed visitors who paid admission to see his experiments. In 1905 a one-hour visit to the Sebastopol, California, experiment farm cost $10.

Burbank was twice married but had no children. He was laid to rest under a cedar of Lebanon tree he had planted from seed in front of his original home place. In death, he said, he should like to feel that his strength was flowing into the strength of the tree.

Burbank's birthday continues to be celebrated as Arbor Day in California. His legacy lives on in the form of hundreds of useful plants that benefit the world today and in his example of a man who lived a life true to his beliefs. SEE ALSO AGRICULTURE, HISTORY OF; BREEDER; BREEDING; HYBRIDS AND HYBRIDIZATION.

Rebecca Baker

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Cacao

C

As currency, beverage, and divine plant, cacao (*Theobroma cacao*, family Sterculiaceae) has played an important role in ancient Central American cultures. To the Mayans, the plant was a gift from their gods—implied in the name *Theobroma*, Latin for "food of the gods." The dried seeds were important in Aztec society as a unit of currency (used in the Yucatan Peninsula until the 1850s), and as part of a drink reserved for the nobility. Today, cacao is probably best known for the sweet, rich food produced from the seeds called chocolate.

Cacao is typically a small- to medium-sized deciduous tree of the New World tropical forests. The small, cream-colored flowers are produced directly from the woody trunks and branches of the tree, not in the leaf axils, where most other flowering plants produce flowers. Following pollination, pods are produced, ranging in color from green through yellow to red-brown. Each pod contains between twenty and sixty seeds that are surrounded by a thick, whitish pulp. Seed dispersal in the wild is usually by monkeys.

Although presently distributed throughout Central America due to migration and dispersal by the Mayans, cacao is thought to have its origin in the eastern Andes. **Cultivation** has led to the production of two

cultivation growth of crop plants

A harvester in Ecuador selects the seeds from cacao pods to use in making chocolate.

forms of cacao: *Criollo*, from Central America, and *Forastero*, from South America. *Trinitario* is a form produced by breeding criollo and forastero types. At the turn of the twenty-first century, cacao is grown commercially in parts of West Africa, Malaysia, Brazil, Central America, and parts of Mexico.

Processing Cacao

The process of producing chocolate from cacao seeds is complex. Following harvesting, ripe pods are opened, the seeds removed, and the pulp scraped away from the seeds. At this point, the light-brown seeds have no discernible chocolate taste. Piles of cleaned seeds are allowed to ferment for up to one week, during which time the chocolate flavor begins to develop as polyphenols start to break down. During the fermentation process, the embryos of the seeds are killed and any remaining pulp is broken down. The color of the seeds also changes to purple. Following fermentation, the seeds are dried, sorted, and shipped to processing factories.

At the processing factory, roasting the seeds removes any remaining water and acids and allows the chocolate flavor to develop. Roasting is done at 121°C for seeds used to produce chocolate, higher for cocoa powder. The roasted seeds are then cracked and the seed coats removed, leaving the cotyledons (known as chocolate nibs), which are then ground using rollers.

During the grinding process, sufficient heat is generated to melt fats in the chocolate nibs, producing a fine paste called chocolate liquor. Baking chocolate is molded, set chocolate liquor. Subjecting the nibs to high pressure prior to grinding removes up to 30 percent of the fats and yields a dry cocoa powder. The fats are called cocoa butter, and they may be used later in the production procedure. Most chocolate is treated with alkalis to neutralize organic acids that are still present in the chocolate. This process, called dutching, produces a mild, dark chocolate.

Milk chocolate is produced by adding condensed milk to chocolate liquor. Stirring the chocolate results in very finely ground cacao particles, which yields a very smooth chocolate. Finally, the addition of extra cocoa butter produces some of the smoothest and creamiest of chocolates.

Chocolate acts as a mild stimulant due to the presence of the alkaloids theobromine, caffeine, and theophylline. The caffeine can be extracted from the discarded seed coats and used in drinks and medicines; extracted theobromine can also be chemically converted into caffeine. SEE ALSO ALKALOIDS; ECONOMIC IMPORTANCE OF PLANTS.

Charles A. Butterworth

Cacti

The members of family Cactaceae are a group of dicotyledonous flowering plants that are primarily native to various dry or seasonally dry habitats in North and South America. Due to the presence of specialized fleshy stems, they are classified as stem succulents. Leaves are not produced in most species, although there are some leafy species in a few genera. There are more than sixteen hundred species of cacti, which are contained in approximately one hundred genera. All cacti share the unique **morphological** features of having most, if not all, of their secondary stems condensed into structures called areoles. These are the places on the stems from which the spines develop. Spines are modified leaves that have become hardened and sharp, thereby providing protection for the plants from **herbivores** in addition to providing some shade to the stems.

morphological related to shape

herbivore an organism that feeds on plant parts

Morphological Adaptations

The plant body of a typical cactus is composed of one or more stem segments that are succulent—that is, having water storage tissue (parenchyma) in their central portions—and a photosynthetic outer skin that is covered by a thickened epidermis and a thick layer of waxy **cuticle**. At various places upon these stem segments are areoles from which both spines and flowers arise. In some columnar and barrel cacti, the stems have developed ribs that assist the plant by providing more surface area to encour-

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

Saguaro cacti in the Sonoran Desert of Arizona.

xerophytes plants adapted for growth in dry areas

crassulacean acid metabolism a water-conserving strategy used by several types of plants

biomass the total dry weight of an organism or group of organisms

age heat loss, to accommodate rapid stem diameter increases following uptake of large amounts of water during rare rain events, and to provide shade in some species. Almost all cacti are **xerophytes** and have evolved adaptations to conserve water that is typically scarce in the habitats they occupy. These anatomical adaptations, in addition to the evolution of **crassulacean acid metabolism** for carbon fixation, have enabled the cacti to flourish in otherwise inhospitable habitats. Some cacti have even become geophytic, with the largest portions of their **biomass** below ground, where they store water in enlarged roots; the aboveground photosynthetic stems are small by comparison.

Geographic Distribution and Ecological Role

Cacti are widely distributed throughout both North and South America, having maximal centers of diversity in the Sonoran and Chihuahuan Deserts of North America, the central Andean region (including Chile, Argentina, Bolivia, and Peru), and the dry scrub forests of eastern Brazil (the Caatinga) in South America. In many habitats, cacti play an important role in the ecology of the region and are often a major component of the arid zone flora in New World deserts. Nearly all forms of animal-mediated pollination syndromes are found in the cacti, with insect (bee and beetle), hummingbird, hawkmoth, and bat pollination types found in species from both North and South America. This accounts for the wide range of variation in floral morphologies seen in various groups of cacti throughout their range.

Diversity

Classification of the cactus family is considered to be highly problematic and difficult due to the effects of convergent or parallel evolution. Systematic studies have shown that there are four major **lineages** of cacti that are recognized at the subfamily rank. Of these, the two primitive groups (*Maihuenia* [two species] and *Pereskia* [sixteen species]) are found mainly in South America and have persistent true leaves, a limited degree of succulence, and are not as well adapted to heat and water stress as are members of the two remaining groups, the subfamilies Opuntioideae and Cactoideae.

lineage ancestry; the line of evolutionary descent of an organism

The *Opuntia* group has approximately three hundred species of cacti or more, and typical members of subfamily Opuntioideae have well-defined stem segments, an unusual kind of specialized seed structure, and a unique type of reverse-hooked small spines (glochids), which penetrate the skin and are easily dislodged from their attachment points in the areoles. These cacti include the prickly pears and chollas (pronounced CHOY-yas), which produce showy flowers that are often pollinated by bees, and develop fleshy (occasionally dry) edible berries called tunas. This group is the most widespread of any in the Cactaceae, ranging from southern Canada southwards almost continuously to the cold habitats of Patagonia in southernmost Argentina. They are found from sea level to high elevation (4,000 meters and higher) and have adapted to a wide variety of habitat types. Species of *Opuntia* introduced into suitable habitats in Africa and Australia have become noxious invasive pests, and removing these escaped cacti has become an significant ecological concern.

The largest subfamily of the cacti (subfamily Cactoideae) contains approximately thirteen hundred species and provides examples of extreme morphological variation in the family. There is a tremendous range of variation in spine form and color, flowering types, formation of ribs and tubercles, and other morphological characters in members of this subfamily. Plants in this group range from plants with narrow upright stems that sometimes branch (a columnar habit) to plants with globular or ball-shaped forms (the barrel cactus types) to **epiphytic** plants that either hang from trees in a pendant fashion (such as in *Schumbergera* or *Rhipsalis*) or are lianas and climb up the surfaces of trees with a vining habit. The most easily recognizable cactus species, the saguaro (*Carnegiea gigantea*), is the state flower of Arizona and the symbol of the American desert. It is also among the tallest of all cacti, with individual plants recorded over 15 meters (50 feet) in height. Some cacti produce special alkaloid **compounds**, notably the peyote cactus (*Lophophora williamsii*), which is known for its **hallucinogenic** properties.

epiphytes plants that grow on other plants

compound a substance formed from two or more elements

hallucinogenic capable of inducing hallucinations

Horticultural Interest

Due to their extreme morphological diversity and their ability to tolerate a wide range of growing conditions, the cacti have received much interest by horticulturists since they were first brought to Europe by Christopher Columbus in the 1490s. The Indian fig, or *Opuntia ficus-indica*, is now widely cultivated throughout the Mediterranean region and in other places for its tasty and sweet multiseeded berries. Other species of cacti are grown for food for humans: nopales/nopalitos are young *Opuntia* stems, while the dragon fruit favored by southeast Asians is the berry of an epiphytic cactus, *Hylocereus undatus*, originally from Central America. Perhaps the most widely grown cactus is also an epiphyte, originating from mountainous regions in south central Brazil. The Christmas cactus (*Schlumbergera*, or *Zygocactus truncata*), often sold during holiday times in winter, is a freely flowering epiphytic cactus that was selected for its showy flowers and ease of cultivation. Tens of thousands of cactus horticulturists around the world collect a wide variety of cacti as a hobby, and a number of international and national societies have been established to promote the understanding, cultivation, and conservation of cactus species. SEE ALSO DESERTS; DICOTS; PHOTOSYNTHESIS, CARBON FIXATION AND; DEFENSES, PHYSICAL; RECORD-HOLDING PLANTS; SUCCULENTS.

Robert S. Wallace

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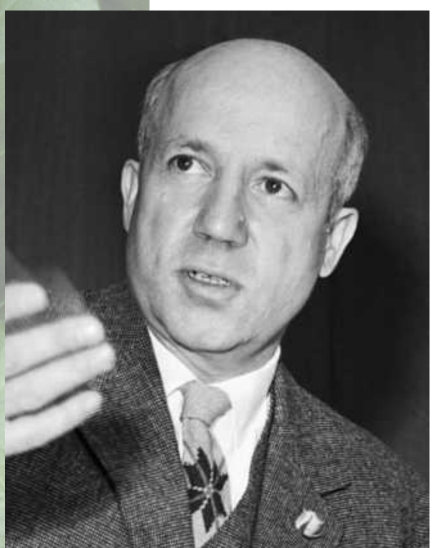
Calvin, Melvin

American Biochemist
1911–1997



Melvin Calvin.

Melvin Calvin was a biochemist whose prolific career included fundamental work on the biochemistry of photosynthesis. His work led to a Nobel Prize and had *Time* magazine calling him "Mr. Photosynthesis."

Calvin was born in St. Paul, Minnesota, on April 8, 1911, of immigrant parents. The family moved to Detroit, Michigan, where Calvin graduated from high school in 1927. He graduated from the Michigan College of Mining and Technology (now Michigan Technological University) as its first chemistry major in 1931. He received his Ph.D. from the University of Minnesota in 1935. He worked two years at Manchester University with British chemist and philosopher Michael Polanyi (1875–1946), who introduced him to the multidisciplinary approach that later characterized his own scientific career.

In 1937 Calvin became an instructor at the University of California at Berkeley and remained there for the rest of his career. He eventually became a professor (1947), director of the Laboratory of Chemical Biodynamics (1963), and associate director of the Lawrence Radiation Laboratory (1967; now the Lawrence Berkeley Laboratory).

compound a substance formed from two or more elements

Together with American physical chemist Gilbert Newton Lewis (1875–1946), Calvin studied the color of organic **compounds**, which introduced him to the importance of the electronic structure of organic molecules. He collaborated with chemist G. E. K. Branch and cowrote *The Theory of Organic Chemistry* (1941), the first American book on the subject to use quantum mechanics.

In 1942 Calvin married Genevieve Jemtegaard, a juvenile probation officer who spent a great deal of time in her husband's laboratory, both assisting and collaborating with him. After their first child died of Rh incompatibility they sought to determine the chemical factors causing the illness. After the 1973 oil embargo they sought new fuel sources from plants (e.g., the genus *Euphorbia*) to convert solar energy into hydrocarbons, an economically unsuccessful project.

During World War II (1939–41) Calvin devised a method for obtaining pure oxygen from the atmosphere onboard destroyers or submarines. He purified and decontaminated the irradiated uranium in fission products and isolated and purified plutonium by his solvent extraction process.

After the radioisotope carbon-14 (because of its long-lived radioactivity, it could be used to follow otherwise untraceable chemical reactions) became available, Calvin began his work on the chemical pathways of photosynthesis. This occupied him from 1946 to 1961 and won him the 1961 Nobel Prize in chemistry. He introduced carbon dioxide (CO_2) labeled with carbon-14 as a tracer into a thin, round flask filled with the single-cell green alga *Chlorella pyrenoidosa* in suspension. The apparatus was illuminated, allowing the alga to incorporate the labeled CO_2 into compounds involved in photosynthesis. Calvin isolated and identified the radioactively labeled constituents, thus determining the steps by which CO_2 is converted into carbohydrates. This set of steps is now known as the Calvin-Benson cycle. Using isotopes, he also traced the path of oxygen in photosynthesis.

The Calvin-Benson cycle is named in honor of Melvin Calvin and Andrew Benson.

Calvin worked on chemical evolution and organic geochemistry, and he examined the organic constituents of Moon rocks for the National Aeronautics and Space Administration. His varied research interests also included photochemistry, free radicals, artificial photosynthesis, radiation chemistry, brain chemistry, the molecular basis of learning, and the philosophy of science.

In 1987 Genevieve died of cancer. Because Calvin's personal and professional life had been built around her presence, her loss was a blow from which he never recovered. Calvin died in Berkeley, California, on January 8, 1997, after several years of declining health. SEE ALSO PHOTOSYNTHESIS, CARBON FIXATION AND; PHYSIOLOGIST; PHYSIOLOGY; PHYSIOLOGY, HISTORY OF.

George B. Kauffman

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Candolle, Augustin de

Swiss Botanist
1778–1841

Augustin de Candolle was a Swiss botanist who advanced significant ideas concerning the classification of plants and developed a taxonomic scheme that provided the foundation for much work in taxonomy up to the present.

As did most learned men of science in his day, Candolle trained in medicine, earning a medical degree from the University of Paris in 1804. During this time, he became friends with several other scientific luminaries working in Paris, including the evolutionary theorist Jean-Baptiste Lamarck (1744–1829) and the paleontologist Georges Cuvier (1769–1832). Candolle became an assistant to Cuvier for a time and helped to revise Lamarck's treatise on French flora.

By this time, Candolle had become professionally interested in botany, and in 1806 obtained a commission to conduct a botanical and agricultural survey of France, an endeavor conducted over the next six years. In 1808 he was appointed professor of botany at the University of Montpellier, where he began work on his *Théorie Élémentaire de la Botanique* (Elementary Theory of Botany), published in 1813.

In this work, Candolle laid out his most significant intellectual contribution to plant taxonomy (and in fact coined the word "taxonomy" as well). Candolle believed that a natural classification scheme should be based on the anatomic characteristics of plants, and in particular the positional relations among parts. Candolle argued, for instance, that in the flower, the position of the stamens in relation to the petals provides important information about whether two species are closely or more distantly related: the more similar the arrangement of parts, the more likely the two species are closely related. While strong adaptational pressures might cause two close relatives to diverge in shape, color, or size, the relation of parts—what Candolle called "symmetry"—would not be as likely to change, since these relations reflected a developmental program that would be much more resistant to large evolutionary changes in a short time. While modern taxonomists use other criteria besides those Candolle proposed, his essential insight into the significance of positional relationships remains an important part of the taxonomist's toolbox.

Candolle became professor of natural history at the University of Geneva in 1817, where he remained until his death. He was the first director of the botanical gardens there, and established what is now one of the world's largest herbarium. He expanded on his theories of classification in *Regni vegetabilis systema naturale* (Natural Classification for the Plant Kingdom), published in 1818, and began the most ambitious task of his life, the *Prodromus systematis naturalis regni vegetabilis*, intended to be a descriptive classification of all known seed plants. Candolle's goal was not only to classify every known species, but also to include ecology, evolution, and the **biogeography** of each (Candolle was, in fact, a pioneer in the field of biogeography). Candolle died in 1841 having completed only seven volumes, but the work was carried on by his son, Alphonse de Candolle (1806–1893), and eventually reached seventeen volumes.

biogeography the study of the reasons for the geographic distribution of organisms

Hundreds of individual plant species were first described and named by Augustin de Candolle, including purple coneflower (*Echinacea angustifolia*), the source of the popular herbal remedy echinacea. Genetic studies of *Arabidopsis* have borne out Candolle's belief that positional relationships are deeply embedded in the genetic program. His son Alphonse, in addition to completing the *Prodromus*, was a leading botanist in his own right. Candolle the younger made major contributions to the theory of the origin of cultivated plants, laying out ideas taken up and expanded upon by Russian geneticist N. I. Vavilov (1887–1943), and published an important early work on plant biogeography. SEE ALSO Arabidopsis; Biogeography; Herbaria; Taxonomist; Taxonomy; Taxonomy, History of; Vavilov, N. I.

Richard Robinson

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Cannabis

Cannabis sativa (of the family Cannabaceae) is the Latin name for marijuana and hemp. The cannabis plant has been cultivated and used for many centuries by a variety of cultures, primarily for two distinct purposes. The long, tough fibers of the stem have been (and still are) used for making rope and cloth (hemp). The leaves and flowers produce a resin (marijuana) that has been (and still is) smoked to attain an altered state of consciousness. In the United States and many other countries, possession and use of marijuana is against the law under most circumstances, although a number of changes in these laws have recently been made to allow it to be used for medical treatment in some states.

Cannabis grows as a woody annual plant. It favors deep, well-drained, loamy soils, but can, and does, grow in almost any soil. The fibers of the stem are formed from tough sclerenchyma cells, joined together to make long strands. The leaves are compound, with five to seven serrated leaflets arranged palmately in a fan shape. The flowers, which form at the end of the summer, are separated by sex onto different plants. Full-grown plants can attain a height of ten feet or more, and a breadth of several feet, but when planted for fiber, seeds are sown so thickly that little branching occurs and stems remain very thin.

A budding cannabis plant.

psychoactive causing an effect on the brain

To harvest the fibers, the plants are cut before flowering and left to cure for days to weeks in the field. This allows retting, or rotting of the stem to loosen the fibers. The fiber is extracted by macerating the plant in water and removing the pulp. Hemp fibers, each from three to six feet long, can be corded into a strong and durable rope. Historically, hemp rope pulled the water bucket from the village well, hanged the criminal on the gallows, and outfitted the great sailing ships of the voyages of discovery. Cannabis varieties grown for hemp contain extremely low levels of **psychoactive** substances. Despite this, hemp went largely out of use as a fiber source in the United States during the mid-twentieth century, due mainly to the political difficulties of keeping it in production while marijuana as a drug was being outlawed.

Leaves and flowers are harvested and dried before the plant reaches full maturity, and most commonly before the seeds have set. Female flowers contain more of the active ingredient THC (delta-tetrahydrocannabinol) than either the male flowers or the leaves, and the THC content decreases after fertilization. Because of this, male plants are often removed from stands being grown for their THC. This simultaneously increases the soil nutrients available to the female plants and prevents fertilization of the flowers.

spasticity abnormal muscle activity caused by damage to the nerve pathways controlling movement

Late in the twentieth century in the United States, the legal use of marijuana has been promoted because of its potential for treating several medical conditions, including glaucoma (high fluid pressure within the eye), **spasticity**, and nausea during chemotherapy. Several states, most notably California, have passed "compassionate use" laws that allow patients to legally obtain marijuana for smoking. At the same time, several states are moving forward with legislation to allow fiber hemp to be grown legally, though these efforts will require the cooperation of the U.S. Drug Enforcement Administration. Currently, hemp fiber for use in the United States is imported from Canada, China, and several other countries where it is grown legally. SEE ALSO CULTIVAR; DEFENSES, CHEMICAL; FIBER AND FIBER PRODUCTS; PSYCHOACTIVE PLANTS.

Richard Robinson

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Carbohydrates

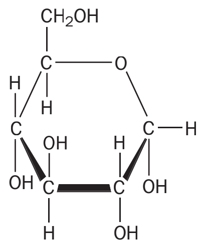
compound a substance formed from two or more elements

empirical formula the simplest whole number ratio of atoms in a compound

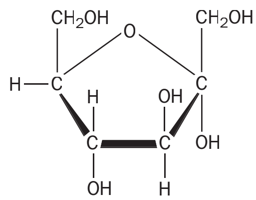
Carbohydrates are a diverse group of **compounds** composed of the elements carbon (C), hydrogen (H), and oxygen (O) with the **empirical formula** $[CH_2O]_n$, where n represents the number of CH_2O units in the compound. The ultimate source of all carbohydrates is photosynthesis, in which the energy of sunlight is used to chemically fix atmospheric CO_2 into carbohydrate. Carbohydrates constitute as much as 80 percent of the dry weight of a plant. This is largely due to the presence of cell walls made of complex carbohydrates surrounding each plant cell.

Sugars, also called saccharides, are carbohydrates. Common sugars occurring in nature have from three (glyceraldehyde) to seven (sedoheptulose) carbon atoms bonded together to form the molecule's backbone. Sugars can be classified chemically as either aldehydes or ketones, and contain OH (**hydroxyl**) groups attached to their carbon backbones. Glucose (an aldehyde sugar) and fructose (a ketose sugar) are two examples of common six-carbon sugars that occur widely in plants. These molecules form ring structures, with glucose forming a six-member ring, and fructose a five-member ring.

hydroxyl the chemical group -OH



D-glucose

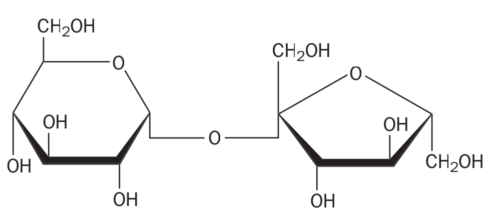


D-fructose

Individual sugars are called monosaccharides. Two sugars linked together chemically are called disaccharides; three are trisaccharides; four are tetrasaccharides, and so on. A generic term for several sugars linked together is oligosaccharide. Molecules with many sugars linked together to form a **polymer** are called polysaccharides. Sucrose (table sugar) is the most abundant disaccharide and is comprised of glucose and fructose. A large amount of sucrose is formed in plant leaves from photosynthetic products. Sucrose is **translocated** over long distances in plants in specialized conductive tissue known as phloem. Sucrose can be broken down, and its components (glucose and fructose) metabolized for energy and as the initial raw material for building cellular components in plant cells distant from photosynthetic leaves. Sucrose also can be stored. High concentrations are found in storage organs such as fruits, sugarcane stems, and enlarged roots of sugar beets. The latter two are commercial sources from which sucrose is refined.

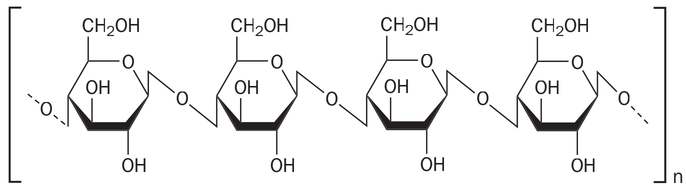
polymer a large molecule made from many similar parts

translocate to move, especially to move sugars from the leaf to other parts of the plant



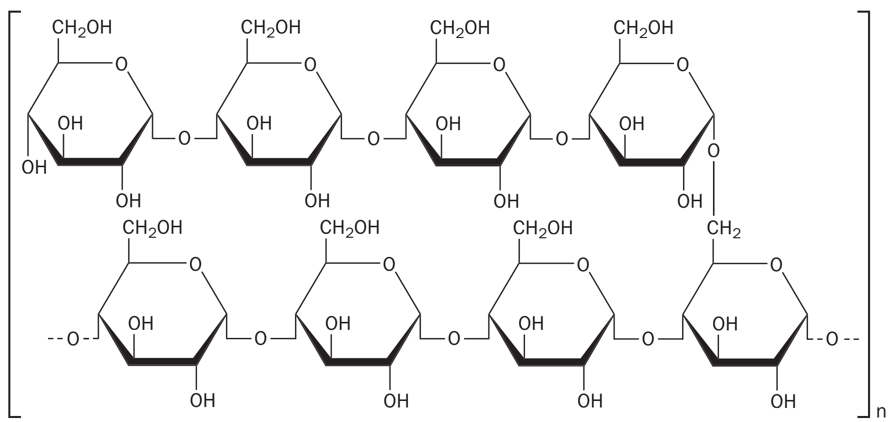
Sucrose

Two important plant polysaccharides, cellulose and starch, are composed exclusively of glucose units bonded together. Cellulose is the most abundant polysaccharide in plant cell walls, and thus, the most abundant polysaccharide on Earth. In cell walls, cellulose occurs along with other complex polysaccharides, each of which is composed of more than one type of sugar. Because of the way glucose is linked in cellulose, individual chains, hundreds of glucose molecules long, are able to bond together by hydrogen bonding in a crystalline arrangement to form a cable-like structure known as a microfibril. These microfibrils are interwoven and give cellulose its strength in plant cell walls and in cotton fabric and paper.



Cellulose

Starch and cellulose differ in the way the glucose molecules are bonded together. Starch is a storage compound in plants, and is broken down as needed into glucose for metabolic use.



Starch

Treatment of denim with cellulase has largely replaced pumice stone in the production of "stone-washed" jeans.

Carbohydrates are important in human nutrition, often constituting the major source of calories in the diet. Glucose, fructose, sucrose, and starch are readily digested by humans. Cellulose and the other complex carbohydrates of the plant cell wall are not readily digested, but constitute useful dietary fiber.

Cellulase, an **enzyme** that can degrade cellulose, is made by many different fungi and some microorganisms. This enzyme allows these organisms to decompose plant material, an important step in the recycling of materials in food webs. SEE ALSO Photosynthesis, Carbon Fixation and; Sugar.

D. Mason Pharr and John D. Williamson

enzyme a protein that controls a reaction in a cell

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Carbon Cycle

All life on Earth is based on carbon, the sixth element of the periodic table. The term carbon cycle refers to the movement of carbon in various forms between Earth's biogeochemical reservoirs: the oceans, the atmosphere, plants, animals and soils on land (the land biosphere), and the geosphere (rocks). Carbon dioxide (CO_2) in the air traps heat, contributing to warming of Earth's surface (called the greenhouse effect) and thereby influencing the climate. Human activities such as burning fossil fuels and clearing forests are causing the amount of CO_2 in the atmosphere to increase rapidly. Concern that global climate change may result has led to a pressing need for scientific research to better understand the global carbon cycle.

The Path of Carbon

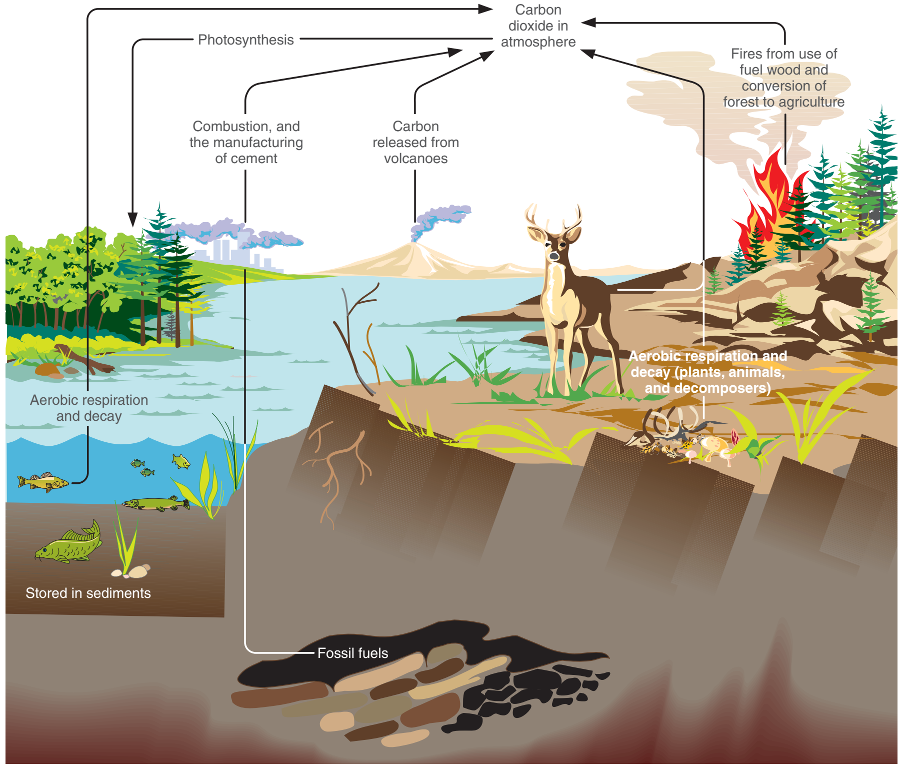
To illustrate some of the important processes of the carbon cycle one can follow a carbon atom as it moves through the biogeochemical reservoirs of the cycle. Begin with a carbon atom that is in the atmosphere in the form of CO_2. In the atmosphere CO_2 is the fifth most abundant gas, behind nitrogen (N_2), oxygen (O_2), argon (Ar), and water vapor (H_2O). Nevertheless, of every million molecules of air, fewer than four hundred are CO_2.

The CO_2 molecule contacts the leaf of an apple tree. It is removed from the air by the process of photosynthesis, also called carbon fixation, whereby plants use light energy from the Sun and water from the soil to convert CO_2 to carbohydrate (sugar) and O_2 gas. The carbohydrate may be converted to other **compounds** that the plant needs to grow and reproduce. The carbon atom may be used by the plant to grow an apple, which may be picked and eaten. The body uses the carbohydrate in the apple for fuel, converting the carbon back into CO_2, which is breathed out to the air. Or, perhaps the apple falls to the ground and gradually rots, meaning that the carbon is converted to CO_2 by decomposers in the soil, including insects, worms, fungi, and bacteria. Either way, this process of converting the carbon in the apple to CO_2 consumes O_2 from the air and is called respiration. About one-tenth of all the CO_2 in the atmosphere is taken up by photosynthesis on land each year, and very nearly the same amount is converted back to CO_2 by respiration. Most of the carbon fixed each year on land is used by plants to make new leaves, which eventually die and fall to the ground where they are decomposed, just like the apple. The rich, dark brown material in the top several centimeters of most soil is mainly decomposing plant material.

compound a substance formed from two or more elements

The CO_2 molecule rides on the wind out over the ocean. It crashes into the ocean surface and dissolves, like sugar dissolving in a glass of water. Since CO_2 is very soluble in water the oceans contain about fifty times as much carbon as the atmosphere. About one-eighth of all the CO_2 in the atmosphere dissolves into the ocean waters each year, but nearly the same amount returns to the atmosphere because the total amount of CO_2 in the ocean is approximately in equilibrium with the amount in the air, and CO_2 is constantly moving into and out of the seawater. The CO_2 molecule, dissolved in the water, is taken up by a single-celled marine plant called a coccolithophore. The carbon is used by the coccolithophore to add to its hard protective coating, which is made of calcium carbonate ($CaCO_3$). When the coccolithophore dies its coating sinks to the bottom of the ocean and becomes part of the marine sediment. Most of the carbon in the sediment is recycled rapidly by respiration or dissolution, but a small amount remains in the sediment and eventually (over millions of years) becomes sedimentary rock.

Being trapped in a sedimentary rock is not the end of the cycle for the carbon atom. If that were the case eventually all of the carbon in the atmosphere, the plants and soils, and the oceans would have ended up in rocks, and the carbon cycle would have stopped long ago. Fortunately, a



The carbon cycle. Note that the geosphere (sedimentary rock) is by far the largest pool of carbon on Earth, but it exchanges only very slowly with the more active pools in the atmosphere, land biosphere, and oceans. Burning fossil fuels represents a huge increase in the transfer of carbon from the geosphere to the atmosphere, causing an increase in the amount of CO_2 in the air (on average 3.1 billion tons of carbon accumulated in the atmosphere each year during the 1990s). More CO_2 in the air drives large net uptake of carbon by the land biosphere and oceans. In pre-industrial times the atmosphere, oceans, and land biosphere were roughly in balance, and net exchanges between these pools were about zero.

little of this carbon is returned to the atmosphere each year, mainly by volcanism. The amount of CO_2 that is emitted by volcanoes and geothermal vents is small, but it is enough to have kept the carbon cycle turning for billions of years.

Following a carbon atom through some pathways of the carbon cycle touches on many important processes. The balance between photosynthesis and respiration on land, the transfer of CO_2 into and out of the oceans, and the incorporation of carbon into sedimentary rocks and return to the atmosphere via volcanic activity all represent recycling of carbon atoms. It is important to understand that the carbon cycle is a dynamic process, it is constantly changing and an adjustment or change in one carbon cycle process will cause changes in many other parts of the cycle. For example, if the amount of CO_2 in the atmosphere increases for some reason, more CO_2 will dissolve into the oceans. Also, since plants require CO_2 as a nutrient, a larger amount of CO_2 in the air will increase plant growth, a process called CO_2 fertilization.

Carbon and Climate

A very important part of the carbon cycle is the influence of CO_2 on Earth's climate. Carbon dioxide is one of several gases in the air (water vapor is the most important one) that trap heat near the surface, causing the surface to be warmed. This process is known as the greenhouse effect. If there were no greenhouse gases in the atmosphere the surface temperature would be about 35°C colder on average than it is, and life on Earth would be very different. More CO_2 means more warming, that is, higher average surface temperature. That means that the amount of CO_2 and other greenhouse gases in the air has a strong influence on the climate of Earth. Furthermore, since many parts of the carbon cycle, such as the plants and soils on land, and the chemistry of the oceans, are sensitive to climate, a change in climate can cause a change in the carbon cycle. For example, in the temperate zone during a warm spring, leaves will come out on the trees earlier than in a cool spring. With a longer growing season the plants can remove more CO_2 from the air, and will grow faster.

Human Influences on the Carbon Cycle

Humans are causing large changes in the carbon cycle. First, humans have altered the land biosphere by cutting forests to clear land for agriculture; for lumber, pulp, and fuel wood; and to make room for cities. Natural grasslands have also been plowed for agriculture. In the early 1990s about 38 percent of Earth's land surface was used for agriculture including croplands and pastures, according to United Nations statistics. When land is cleared, most of the carbon stored in the plants and much of that stored in the soils is converted to CO_2 and lost to the atmosphere. Second, since the mid-1800s humans have learned to harness the energy stored in fossil fuels, mainly coal, oil, and natural gas. The term fossil fuels refers to the fact that these materials are composed of the fossil remains of ancient plants. When fossil fuels are burned, energy that can be used to light and heat our homes, drive our cars, and manufacture all the goods that we use from day to day is released. Burning fossil fuels also consumes O_2 and releases CO_2 to the air. In 1996, 6.5 billion metric tons of carbon were released to the atmosphere from fossil fuels. That's a little more than 1 ton of carbon per person per year worldwide. The use of fossil fuel, however, is not evenly distributed. The United States, with less than 5 percent of Earth's population, used 22 percent of the fossil fuels in 1996, and on a per-person basis residents of the United States used about nineteen times as much fossil fuel as the residents of Africa. The use of fossil fuels is growing rapidly, particularly in developing countries such as China.

Carbon dioxide from fossil fuels and land clearing caused a 25 percent increase in CO_2 in the atmosphere between the eighteenth century and the 1990s. Only about one-half of the CO_2 that has been emitted into the atmosphere has remained there, the rest has been taken up by the oceans and the land biosphere. Scientists do not know exactly how much of the added CO_2 has gone into the oceans and how much has gone into the land biosphere, nor do they understand precisely why the land biosphere is taking up a lot of CO_2. One reason that the land biosphere may be taking up carbon is the CO_2 fertilization effect mentioned above. Another explanation is that forests that were cleared for agriculture and lumber in the 1800s and early 1900s may be regrowing. These are important questions for future research. The answers will affect our ability to regulate the amount of CO_2 in the atmosphere in order to lessen climate change.

Burning fossil fuels represents a huge increase in the transfer of carbon into the atmosphere from sedimentary rocks in Earth's crust. Unless an alternative source of energy is found, it is likely that in a few hundred years humans could burn all of the coal, oil, and gas that is believed to exist on Earth, and that took many millions of years to form. If this occurs the amount of CO_2 in the atmosphere will be several times the preindustrial amount,

saturate containing as much dissolved substance as possible

dissipate to reduce by spreading out or scattering

and the oceans will become completely **saturated** with CO_2, which would drastically alter their chemical composition. Also, the increased greenhouse effect would cause very substantial but currently unpredictable changes in climate. Because the leak of carbon out of the oceans and atmosphere into the sediments and eventually into the sedimentary rocks is very slow, the added carbon would take thousands of years to **dissipate** from the oceans and atmosphere. SEE ALSO BIOGEOCHEMICAL CYCLES; DECOMPOSERS; GLOBAL WARMING; HUMAN IMPACTS; PHOTOSYNTHESIS, CARBON FIXATION AND.

Peter S. Bakwin

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Carnivorous Plants

Plants that trap and digest tiny animals have fascinated people for centuries. It was known by 1790 that sundews, pitcher plants, and the Venus's-flytrap could catch insects. This interest led Thomas Jefferson to collect Venus's-flytraps near Charleston, South Carolina, for study. A century later, Charles Darwin referred to the Venus's-flytrap as one of the most wonderful plants in the world. More recently, certain adventurous, twentieth-century Hollywood movies depicted man-eating plants as inhabiting mysterious tropical jungles. Carnivorous plants, in fact, are relatively small and do not live in dark swamps and jungles, and the largest animal ever found trapped in one of the plants was a small rat. Carnivorous plants catch mostly insects, and hence are often referred to as insectivorous plants.

Carnivorous plants are defined as plants that attract, catch, digest, and absorb the body juices of animal prey (referred to as the carnivorous syndrome). The major types of carnivorous plants are sundews, pitcher plants, butterworts, bladderworts, and the unique Venus's-flytrap. More than 150 different types of insects have been identified as victims, but also arachnids (spiders and mites), mollusks (snails and slugs), earthworms, and small vertebrates (small fish, amphibians, reptiles, rodents, and birds) are known to have been caught.

Many different kinds of plants have insect-attracting structures such as colorful leaves and flower parts and produce sweet sugar secretions (like nectar). Others may ensnare and kill small animals using sticky hairs, thorns, cupped leaves, poisonous liquids, or a combination of these tactics. In some cases it is known that the juices of dead animals can be absorbed through the surfaces of plant leaves. However, only true carnivorous plants have the ability to obtain nutrients from animal prey.

It is known that carnivorous plants can survive without catching prey. However, botanists believe that the added nutrition derived from carnivory helps the plants grow faster and produce more seeds, thus allowing the plants to survive better and spread into new areas. In general, carnivorous plants grow in poor soils where nitrogen, phosphorus, and potassium are lacking.

MAJOR CARNIVOROUS PLANT GROUPS

Genus	Common Name	Number of Species (approximate)	Geographical Distribution
Sarracenia	Trumpet pitcher plant	10	Southeastern United States, with one species extending across Canada
Darlingtonia	California pitcher plant	1	Northern California and adjacent Oregon
Heliamphora	South American pitcher plant	5	Venezuela, Guyana, Brazil
Nepenthes	Tropical pitcher plant	75	Southeast Asian tropics, from Australia, Malaysia, and India to Madagascar
Cephalotus	Australian pitcher plant	1	Western Australia
Drosera	Sundew	110	Worldwide, especially South Africa and Australia
Dionaea	Venus's-flytrap	1	Southeastern North Carolina and adjacent South Carolina
Pinguicula	Butterwort	60	Mostly Northern Hemisphere
Utricularia	Bladderwort	200	Worldwide

They obtain these nutrients, especially nitrogen and phosphorus, from their prey, and they are quickly absorbed through the leaf surface and transported throughout the plant. Although carnivorous plants do absorb nutrients from a weak fertilizer, for instance, high concentrations of fertilizer, as are suitable for garden crops and houseplants, normally kill carnivorous plants.

Habitats

There are more than 450 different species of carnivorous plants found in the world. At least some occur on every continent except Antarctica. They are especially numerous in North America, southeastern Asia, and Australia. Carnivorous plants typically live in wet habitats that are open and sunny, with nutrient-poor soils having an acidic **pH**. They do not like competition from other plants, and thus seem to thrive in the nutrient-poor habitats where other types of plants do not grow very well. These plants may be found in wet meadows in the southeastern United States or in peat-moss bogs in northern North America and Eurasia. Some are true aquatics, growing in the quiet waters of ponds and ditches around the world. Still others grow on wet, seeping, rocky cliffs or moist sand. In many cases they grow in places that have periodic fires that act to cut down on competition, keep their habitats open, and release nutrients into the soil.

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral; low pH numbers indicate high acidity; high numbers indicate alkalinity

Types of Traps

The traps of carnivorous plants are always modified leaves. They may be active or passive in their mechanism. Active traps have sensitive trigger hairs and moving parts, such as the sticky, glue-tipped hairs that cover the leaves of sundews. The paired leaf blades of the Venus's-flytrap snap shut like jaws when trigger hairs are touched inside. The aquatic bladderworts have little inflated pouches that suck in microscopic animals and mosquito larvae. The passive traps of terrestrial butterworts consist of flat leaves covered with a greasy, sticky surface that are effective at catching crawling insects much like flypaper traps flies. The elegant pitcher plants have passive pitfall traps that are hollow, tubular leaves. Insects fall in, die, and sink to the bottom to be digested. The hoods on most pitcher plants keep out rainwater and prevent prey from flying out. In many cases, especially in pitcher plants that hold water, bacteria may aid in digesting prey. It is also known that several species of mites and fly larvae live inside the trumpet leaves of

An oblong-leaved sundew flower (*Drosera intermedia*) traps a white-legged damselfly.

pitcher plants, without themselves being harmed, and help break down prey for digestion. Pitcher plants may be terrestrial, growing in clumps of erect pitcher leaves (such as the *Sarracenia* pitcher plants) in the North American temperate zone, or they may grow as sprawling vines in the Malaysian tropics, with pitchers hanging from the tips of their flat leaf blades (such as the *Nepenthes* pitcher plants).

Microscopic glands are present on each type of trap. They are specialized cells that perform various jobs. They may act as receptors to detect the presence of prey, or they may secrete digestive fluids to dissolve the animal bodies with only the outer shell of **chitin** of arthropods (insects, spiders, and their relatives) remaining undigested. The glands also absorb the products of digestion, taking them into the leaves of the plant. For example, the sticky hairs of the sundew trap the insect and slowly curve over to press the victim onto the leaf surface where digestive juices are secreted and nutrients absorbed.

chitin a cellulose-like molecule found in the cell wall of many fungi and arthropods

While a variety of carnivorous plants are scattered around the world, the area with the most numerous types is the Green Swamp Nature Preserve in southeastern North Carolina (Brunswick County). Occurring in this area are four species of *Sarracenia*, four species of *Drosera*, ten species of *Utricularia*, three species of *Pinguicula*, and the single species of *Dionaea*. SEE ALSO EVOLUTION OF PLANTS; INTERACTIONS, PLANT-INSECT; PEAT BOGS; WETLANDS.

T. Lawrence Mellichamp

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Carotenoids

The carotenoids are red, orange, and yellow pigments synthesized by all green plants and some microbes. They have an essential function in photosynthesis and in attracting the attention of animals. Several of these pigments also have an important nutritional function for animals and some of the familiar colors of animals are derived from plant or microbial carotenoids they consume.

Structure and Occurrence

Carotenoids are synthesized in the plastids of a plant cell and typically contain forty carbon atoms derived from eight subunits of the five-carbon compound, isoprene. Larger and smaller carotenoids do occur. Two categories of carotenoids occur in nature. These are the carotenes that contain only carbon and hydrogen, and the xanthophylls (also termed oxycarotenoids) that contain carbon, hydrogen, and oxygen atoms. Each carotenoid has its own distinctive color. Their chemical structure makes carotenoids very insoluble in water, but they are fat-soluble. Therefore they are usually associated with cell membranes and lipids, the primary water-insoluble component of cells. Some plant carotenoids occur as crystals in a protein matrix, and in some animals carotenoids occur with proteins. These animal carotenoproteins can be a very different color than their component carotenoids. For example, the carotenoprotein responsible for the distinctive blue color of some live lobsters breaks into a bright red carotenoid and colorless protein upon heating. Over six hundred carotenoids occur in plants, animals, and microbes. Since only plants and some microbes can synthesize carotenoids, those carotenoids in animals all come from their dietary sources. Typically several different carotenoids occur in plant tissue containing this class of pigments. For example, orange carrots contain at least six different carotenes that account for their color. All green leaves contain beta-carotene and three xanthophylls, lutein, neoxanthin, and violaxanthin. Most leaves also contain alpha-carotene and several other xanthophylls as well.

Both chlorophylls and carotenoids occur in all green leaves, but chlorophylls mask the carotenoids to the human eye. When the chlorophylls break down as leaves senesce (mature), the yellow and orange carotenoids persist and the leaves turn yellow.

Role in Plants

In the process of photosynthesis, potentially harmful oxidizing **compounds** are generated. The carotenoids occur in photosynthetic tissues along with chlorophyll to protect them from **photooxidative** damage. In fact, this protection is essential for photosynthesis. The photoprotective role of carotenoids is demonstrated in plant mutants that cannot synthesize essential leaf carotenoids. These mutants are lethal in nature since without carotenoids, chlorophylls degrade, their leaves are white in color, and photosynthesis cannot occur. Carotenoids also assist chlorophylls in harvesting light. Carotenoids absorb wavelengths of blue light that chlorophylls do not. The energy that carotenoids harvest in the blue range of the spectrum and transfer to chlorophyll contributes significantly to photosynthesis. The growth and development of plants is often stimulated by light, and

compound a substance formed from two or more elements

photooxidize to react with oxygen under the influence of sunlight

A carrot harvest. Carrots contain at least six different carotenes that account for their color.

carotenoids have sometimes been implicated as the photoreceptors of light to trigger these responses.

Outside of photosynthesis, plant carotenoids also serve as one of the pigments, along with anthocyanins and betalains, that provide color to flowers, ripening fruit, and other plant parts. Familiar examples of carotenoids having this role are found in sunflowers, marigolds, bananas, peaches, oranges, tomatoes, peppers, melons, and yellow corn. Two root crops, carrots and sweet potatoes, also acquire their color from carotenoids. These colors attract insects, birds, and bats for pollinating flowers, and they attract a wide range of animals to aid in the dispersal of seeds and fruits.

Role in Animals

Beyond their role in attracting animals, carotenoids are important nutrients and colorants for animals that consume them. Vitamin A is an essential nutrient for humans and animals, and all vitamin A ultimately comes from dietary carotenoids. A small subset of all carotenoids, including beta-carotene, can be converted to vitamin A by animal metabolic systems. Animals cannot synthesize these provitamin A carotenoids or vitamin A itself from scratch, and humans around the world obtain about two-thirds of their vitamin A in this provitamin form from plants they eat. The rest is consumed as vitamin A from meat, eggs, and dairy products that ultimately came from carotenoids in the diets of these animal sources.

Genetic engineering of rice may allow high expression of carotenoids. However, the normally white rice becomes yellow-orange in the process, which may not be appealing to consumers.

Animal products and tissues containing vitamin A, which has no color, often contain carotenoids as well. This is the case in egg yolk, butterfat, and the pink or red flesh color of certain fish, such as salmon and trout. Dietary carotenoids are readily visible in the striking and familiar colors of flamingoes, canaries, lobsters, prawn, goldfish, and ladybugs. Some of the coloration in human skin is also due to the carotenoids consumed. Beyond their important role as a source of vitamin A for humans, dietary carotenoids, including those that are not provitamin A carotenoids, have been implicated as protecting against certain forms of cancer and cardiovascular disease. Two carotenoids that appear to impart health benefits are lycopene and lutein.

Lycopene is the red carotene that accounts for the typical color of tomatoes and watermelon. Lutein is a yellow xanthophyll common in all green leaves and responsible for much of the color of milk, butter, and egg yolks. The **antioxidant** properties that make carotenoids essential for photosynthesis may provide a similar type of protection in preventing human disease.

antioxidant a substance that prevents damage from oxygen or other reactive substances

Commercial Importance

The color of food is an important variable contributing to its selection for consumption. Carotenoids in plant extracts such as red palm oil, saffron, annatto, and paprika have been used as food colors through much of history. More recently, industrially produced (synthetic) carotenoids have also been used as food color. Poultry, fish, and mammalian food animal diets also are frequently supplemented with natural or synthetic carotenoids to not only provide a dietary vitamin A source, but primarily to color meat and animal products and make them more appealing for consumers. Medicines and cosmetic products are often colored with carotenoids to enhance their appeal. SEE ALSO PIGMENTS; PLASTIDS.

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Carver, George Washington

American Botanist
1865–1943

George Washington Carver was born in 1865, near the end of the Civil War (1861–65). His mother was a slave on the Moses and Susan Carver farm close to Diamond Grove, Missouri. Carver was orphaned while still in his infancy and was raised by the Carvers. He received a practical education working on the farm and in 1877 was sent to attend a school for African-American children in the nearby town of Neosho. From Neosho, Carver traveled through several states in pursuit of a basic education. He took odd jobs to support himself and lived with families he met along the way.

George Washington Carver.

In 1890 Carver began a study of art at Simpson College in Indianola, Iowa. The following year he left Simpson to pursue studies in agriculture at the Iowa State College of Agriculture and Mechanic Arts in Ames. He enrolled in 1891 as the first African-American student at Iowa State. Carver maintained an excellent academic record and was noted for his skill in plant **hybridization** using techniques of cross-fertilization and grafting. An appointment as assistant botanist allowed him to continue with graduate studies while teaching and conducting greenhouse studies.

hybridization formation of a new individual from parents of different species or varieties

In 1896 American educator Booker T. Washington (1856–1915) extended an invitation to Carver to head the agriculture department at Alabama's Tuskegee Institute. Carver accepted the invitation and remained at Tuskegee until his death forty-seven years later in 1943. During his tenure at Tuskegee he taught classes, directed the Agricultural Experiment Station, managed the school's farms, served on various councils and committees, and directed a research department.

Carver's work focused on projects that held potential for improving the lives of poor southern farmers. Years of repeated planting of a single crop, cotton, and uncontrolled erosion had depleted southern soils. He advocated the wise use of natural resources, sustainable methods of agriculture, soil enrichment, and crop diversification.

One of Carver's first efforts was to find methods within reach of the farmer with limited technical and financial means for enriching the soils. He conducted soil analysis to determine what was needed to make soils more productive. Then Carver proceeded to set up scientific experiments to determine organic methods for building up the soil. He also tried planting and cultivating various plants and plant varieties so he could identify ones that could be successfully grown. Sweet potatoes, peanuts, and cowpeas were considered the most promising. These plants were favored because they could help enrich the soil, they could offer good nutritional value to animals and humans, they were easily preserved and stored, and they could be used as raw material for the production of useful products. Carver developed hundreds of products from these resources. He recognized that processing raw materials was a means of adding value to and increasing the demand for the agricultural products of the South.

When the United States entered World War I in 1917, shortages of certain goods were felt. This caused Carver's substitutes and alternatives to gain attention. Sweet potato products and peanut milk were especially of interest. In 1921 Carver appeared before a congressional committee to testify on the importance of protecting the U.S. peanut industry by establishing a tariff on imported peanuts, and a tariff was established. This event brought Carver national and international recognition as a scientist. Carver spent the remainder of his life conducting agricultural research and sharing his knowledge with individuals in the South and throughout the world. SEE ALSO AGRICULTURE, ORGANIC; BREEDER; BREEDING; ECONOMIC IMPORTANCE OF PLANTS; FABACEAE.

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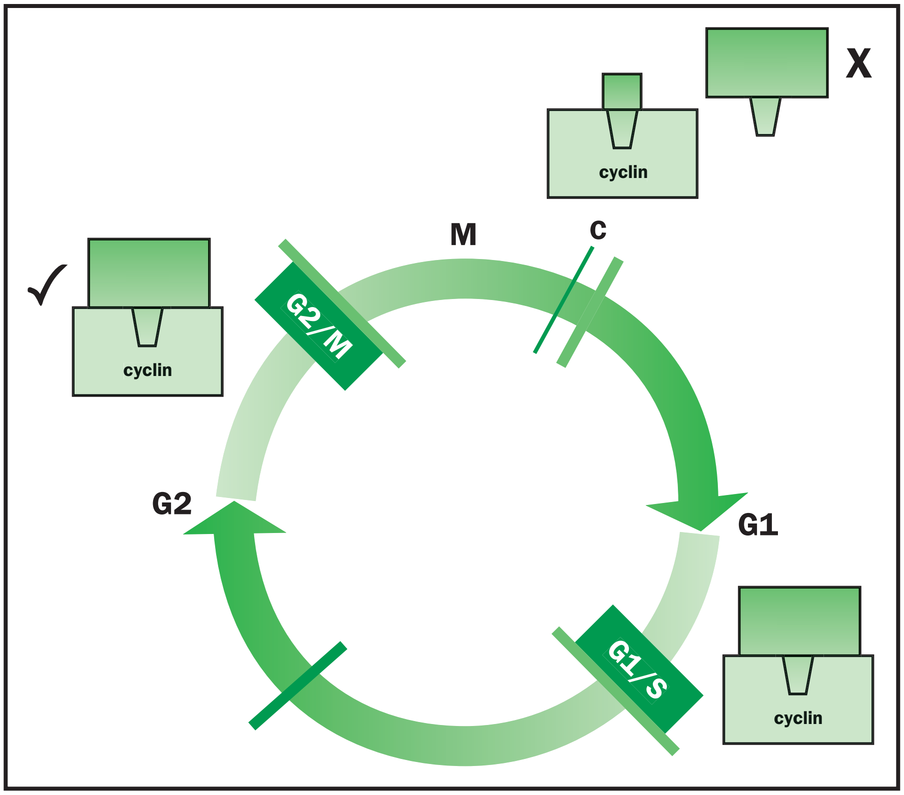
Cell Cycle

During the cell cycle, cells grow, double their nuclear deoxyribonucleic acid (DNA) content through chromosome replication, and prepare for the next mitosis (chromosome separation) and cytokinesis (cytoplasm separation). In effect, the cell cycle is the proliferating cell's life history. Cells spend most of their time in interphase, the period between divisions, acquiring competence for division. For example, in the higher plant *Arabidopsis thaliana* at



An idealized cell cycle, showing the order of mitosis (M), cytokinesis (C), postmitotic interphase (G1), DNA synthetic phase (S-phase), and postsynthetic interphase (G2). Major control points of the cell cycle at G1/S and G2/M are indicated as hatched rectangles. P34 (Cdc2 kinase) is shown bound to a cyclin at G2/M, where it exhibits catalytic activity (✓) while cyclin degrades at M/G1 and Cdc2 stops working (**X**). A Cdc2-cylin complex is also shown at G1/S, but note this is not necessarily the same cyclin as the one at G2/M.

23°C, **meristematic** cells are in interphase for eight hours but are in mitosis for only thirty minutes.

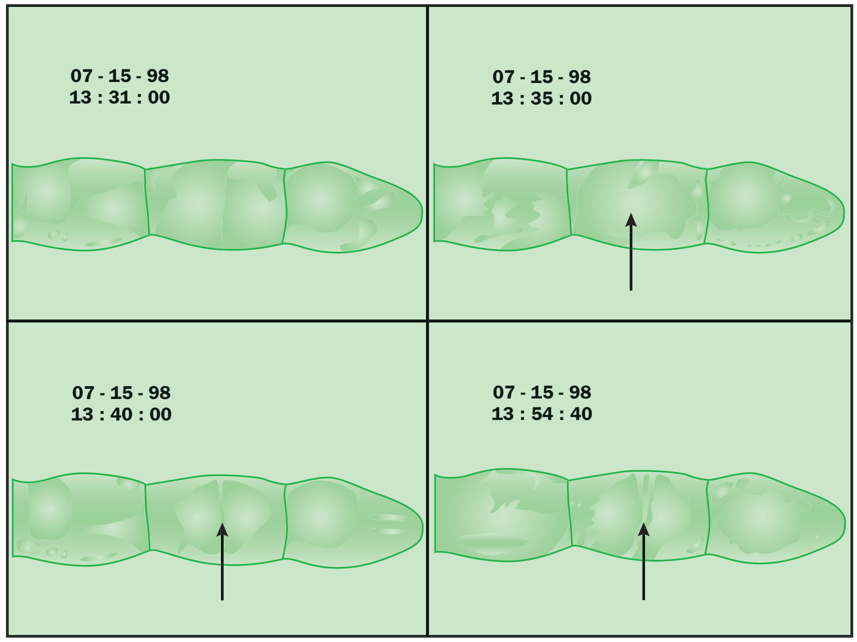
meristematic related to cell division at the tip

The Phases of the Cell Cycle

The cell cycle is commonly described as having four phases: M (mitosis), Gap 1 (postmitotic interphase), S-phase (period of DNA synthesis), and Gap 2 (postsynthetic interphase). Gaps 1 and 2 were initially thought to be resting stages between mitosis and S-phase. This description is a misnomer because numerous genes regulate cell growth in these phases. Appropriately, these terms became abbreviated to G1 and G2. Moreover, networks of cell cycle gene products constitute molecular checkpoints that in G1 determine whether a cell is competent to replicate its chromosomes during S-phase, and that in G2 sense whether the cell is ready to partition its chromatids during mitosis. Uniquely in plant cells, in late G2 an array of microtubules known as the preprophase band appears and chromosomes separate in a plane perpendicular to it.

Only in mitosis do chromosomes become visible by light microscopy; each one appears as two sister chromatids constricted at a specific point along their length, the centromere. At mitosis, a **diploid** parent cell passes through four phases: prophase, metaphase, anaphase, and telophase. During late prophase, the nuclear envelope disintegrates and spindles of microtubules span the cell. Unlike animal mitosis where the spindles attach to centrioles (and associated polar asters), there is no obvious anchoring structure for higher plant spindles. This led to the botanical term "anastral cell division." At metaphase, the chromosomes align at the cell's equator and attach to mitotic spindles via kinetochores, discs of structural protein that also

diploid having two sets of chromosomes, versus having one (haploid)



Arrows point to a developing cell plate, which divides the new daughter cells.

bind to the centromere of the chromosome. During anaphase, sister chromatids are pulled apart and move to opposite ends of the cell. In telophase, nuclear envelopes reform around each new diploid set of chromosomes followed by cytokinesis when a new wall forms between sibling cells. Cytokinesis requires the formation of a cell plate or phragmoplast that spans the cell center, and becomes dense with **vesicles** from the Golgi complex (also called the Golgi apparatus). The plasma membrane and the membrane surrounding the phragmoplast fuse, resulting in separation of the sibling cells. On the phragmoplast, cellulose forms the fibrillar component of the cell wall while hemicelluloses and pectins are added as a matrix. Trapped in the primary cell wall are cytoplasmic strands and microtubules that become plasmodesmata, the cytoplasmic connections between the new cells.

vesicle a membrane-bound cell structure with specialized contents

Regulation

Most knowledge about regulatory cell cycle genes comes from studies of yeasts and vertebrate cells, but the molecular landscape of the plant cell cycle is being identified. In fact, an important discovery about the cell cycle stemmed from work on plant cells in the 1960s by Jack Van't Hof at the Brookhaven National Laboratory in New York. He discovered that when cultured pea root tips were deprived of carbohydrate, meristematic cells stopped dividing and arrested in either G1 or G2. If sucrose and inhibitors of protein synthesis or adenosine triphosphate (**ATP**) synthesis were then added to the medium, the cells continued to arrest in G1 or G2 despite nutrient availability. With confirmatory data from other species, in 1973 Van't Hof published his principal control point hypothesis: that there are two major control points of the cell cycle, one at G1/S and the other at G2/M, both of which are dependent on adequate nutrients, the generation of energy, and protein synthesis. Discovery of the proteins synthesized at these transitions and the genes that encode them occurred in the 1980s. Paul Nurse at the Imperial Cancer Research Fund (ICRF) in London discovered that a fission yeast cell division cycle (cdc) gene, cdc2, was absolutely re-

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells quired for the G2/M and G1/S transitions. Cdc2 encodes a protein kinase, an **enzyme** that catalyzes substrate phosphorylation. Although the kinase (also called p34 because its molecular weight is 34 kilodaltons), is not fully understood, it can phosphorylate lamin proteins that line the inside of the nuclear envelope. Notably, phosphorylated lamins become unstable, leading to nuclear envelope breakdown. Presumably, p34 drives a cell into mitosis at least partly because it phosphorylates lamins. Genes equivalent to cdc2 have been discovered in humans, frogs, insects, fish, and higher plants.

enzyme a protein that controls a reaction in a cell

How does mitosis stop so abruptly when two siblings enter G1, even though p34 is still present? This puzzle was partly solved by Tim Hunt at the ICRF laboratories. A protein extract injected into immature frog oocytes caused them to undergo meiosis prematurely. Hunt noticed one protein in the extract that increased in concentration during the cell cycle but disappeared suddenly at the M to G1 phase transition. It was called cyclin. Data from the fission yeast and frog systems indicated that p34 depends on cyclin for its phosphorylating activity. In fact, p34 and cyclin bind together from late G2 until late mitosis and then, suddenly, cyclin is degraded, p34 stops working, and mitosis ends. Plant-like cyclins have also been identified in various higher plants including *Arabidopsis*, alfalfa, and rice, reflecting remarkable conservation of the key cell cycle genes among unrelated organisms. SEE ALSO CELLS; CELLS, SPECIALIZED TYPES; MERISTEMS.

Dennis Francis

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Cells

Plants are multicellular organisms composed of millions of plant cells. Although individual cells may differ greatly from each other in mature structure, all plant cells share the same basic eukaryotic organization. That is, each plant cell possesses a nucleus and cytoplasm with subcellular **organelles.** In addition to these components, all plant cells possess a cell wall of cellulose. Although plant cells begin their life with a full complement of cellular components, some specialized cell types lose their nuclei and all or part of their cytoplasm as they mature.

organelle a membrane-bound structure within a cell

Components of a Cell

Cell Wall. Plant cells, unlike animal cells, are surrounded by a relatively thin but mechanically strong cell wall. Plant cell walls consist of a complex mixture of **polysaccharides**, proteins, and phenolic **polymers** that are secreted by the **protoplast** and then assembled into an organized network linked together by **covalent** and hydrogen bonds. Cell walls function in the support of plant tissues and in mechanical protection from insects and **pathogens**. Plant cell walls are made up of cellulose microfibrils embedded in an amorphous matrix, an organization analogous to that of fiberglass or steel-reinforced concrete. Cellulose microfibrils consist of linear chains of glucose, with each chain composed of two thousand to twenty-five thousand glucose units. About fifty such chains are linked side by side through

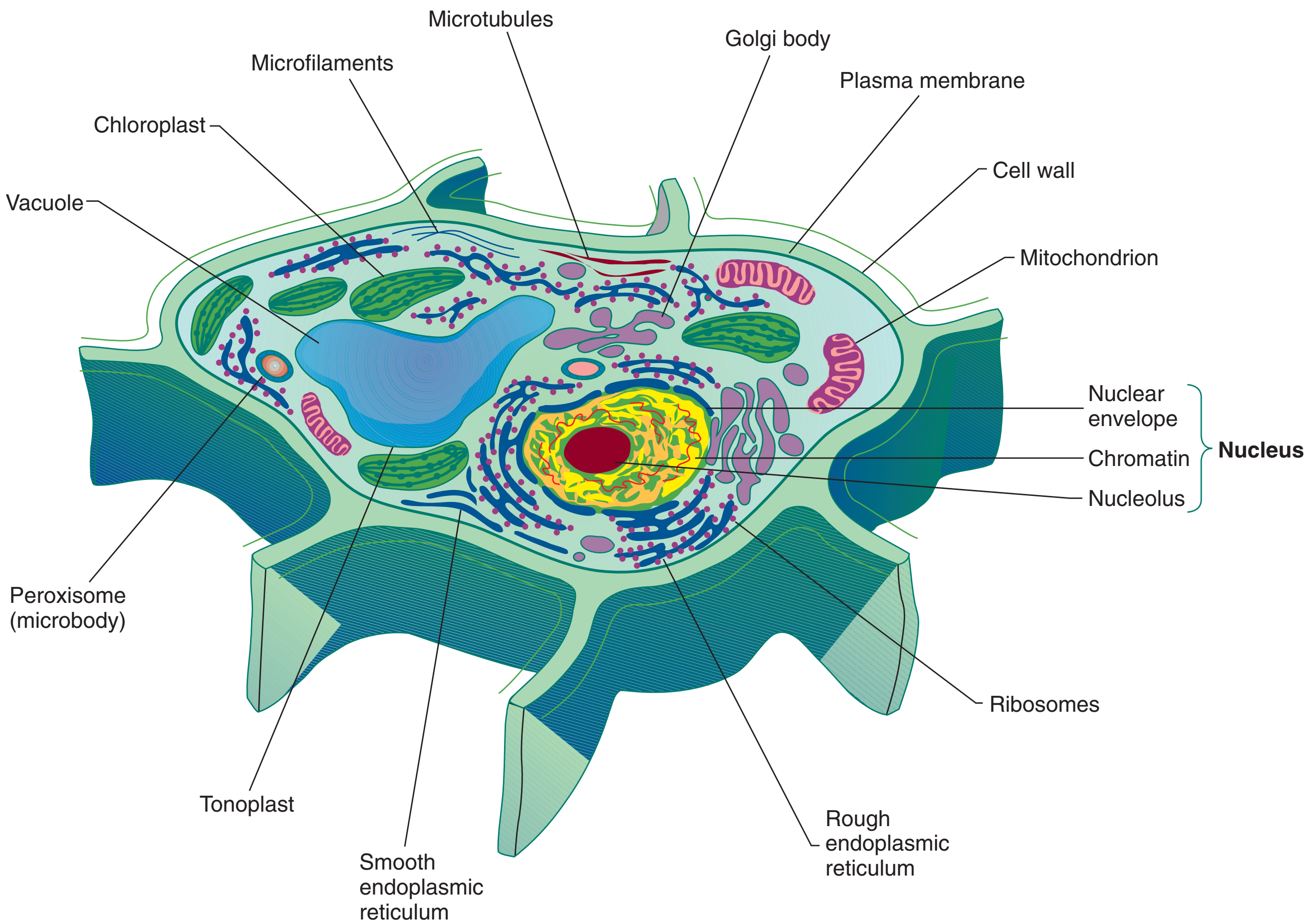
polysaccharide a linked chain of many sugar molecules

polymer a large molecule made from many similar parts

protoplast the portion of the cell within the cell wall

covalent held together by electron-sharing bonds

pathogen disease-causing organism



Components of a plant cell.

hydrogen bonds to form one microfibril. Hydrogen bonding between adjacent glucose units forms highly crystalline regions within the cellulose microfibril, giving cellulose its stiffness and high tensile strength.

Cellulose microfibrils are embedded in a matrix composed of pectin, hemicelluloses, and proteins. Pectins and hemicelluloses are shorter chain polysaccharides that are either branched or unbranched and form cross-links between the cellulose microfibrils. In the presence of calcium ions, pectins form a highly hydrated gel (purified pectin is used in jam and jelly making). Cell wall carbohydrates are covalently linked to cell wall proteins that are rich in the rare amino acid hydroxyproline. Cell wall structural proteins vary greatly in their composition but are thought to provide strength, particularly in cells that are growing.

Specialized types of plant cells such as sclerenchyma fibers and xylem vessels require a hard, rigid cell wall in order to function. These cells synthesize a thick, inner wall layer called a secondary cell wall. The secondary cell wall is impregnated with a polymer of phenolic units called lignin. Lignins are much-branched, long chain phenolic **compounds** that form many cross-links with other wall components and give secondary cell walls great strength and rigidity.

compound a substance formed from two or more elements

Cell Membrane. The portion of the plant cell inside the cell wall is called the protoplast. The protoplast is bounded by a membrane known as the

COMPONENTS OF A PLANT CELL

Component	Number Per Cell (approximate)	Diameter/Thickness	Function
Cell wall	1	1 micrometer	Support, protection
Nucleus	1	10 micrometers	Site of most of cell's genetic information
Endoplasmic reticulum	1 interconnected network	30 nanometers (thickness of cisterna)	Protein synthesis, processing, and storage, lipid synthesis
Golgi apparatus	100	1 micrometer (thickness of cisterna)	Protein processing, secretion
Vacuole	1	100 micrometers	Osmotic regulation, storage
Mitochondrion	200	1 micrometer	Cellular respiration
Plastid	20	5 micrometers	Photosynthesis
Peroxisome	100	1 micrometer	Photorespiration
Microtubule	1000	25 nanometers	Cell shape, cell division
Microfilament	1000	7 nanometers	Chromosome movements, cytoplasmic streaming

cell membrane or the plasma membrane. Like all biological membranes, it consists of a double layer of phospholipids in which proteins are embedded. Phospholipids are a class of lipids in which glycerol is covalently linked to two fatty acids and to a phosphate group. The hydrocarbon chains of the fatty acids are **nonpolar** and form a region that is highly **hydrophobic**. The proteins associated with the lipid layer are of two types: integral and peripheral. Integral proteins span the entire thickness of the lipid layer. For example, the cellulose synthase **enzymes** that catalyze the synthesis of cellulose are integral proteins. They extend across the cell membrane, taking up glucose precursors on the inner side and extruding a cellulose microfibril on the outer side. Peripheral proteins are attached to one surface of the lipid layer. Peripheral proteins on the inner surface of the plasma membrane often function in interactions between the membrane and components of the cytoskeleton. Some peripheral proteins on the outer surface of the plasma membrane function in hormone perception and signaling.

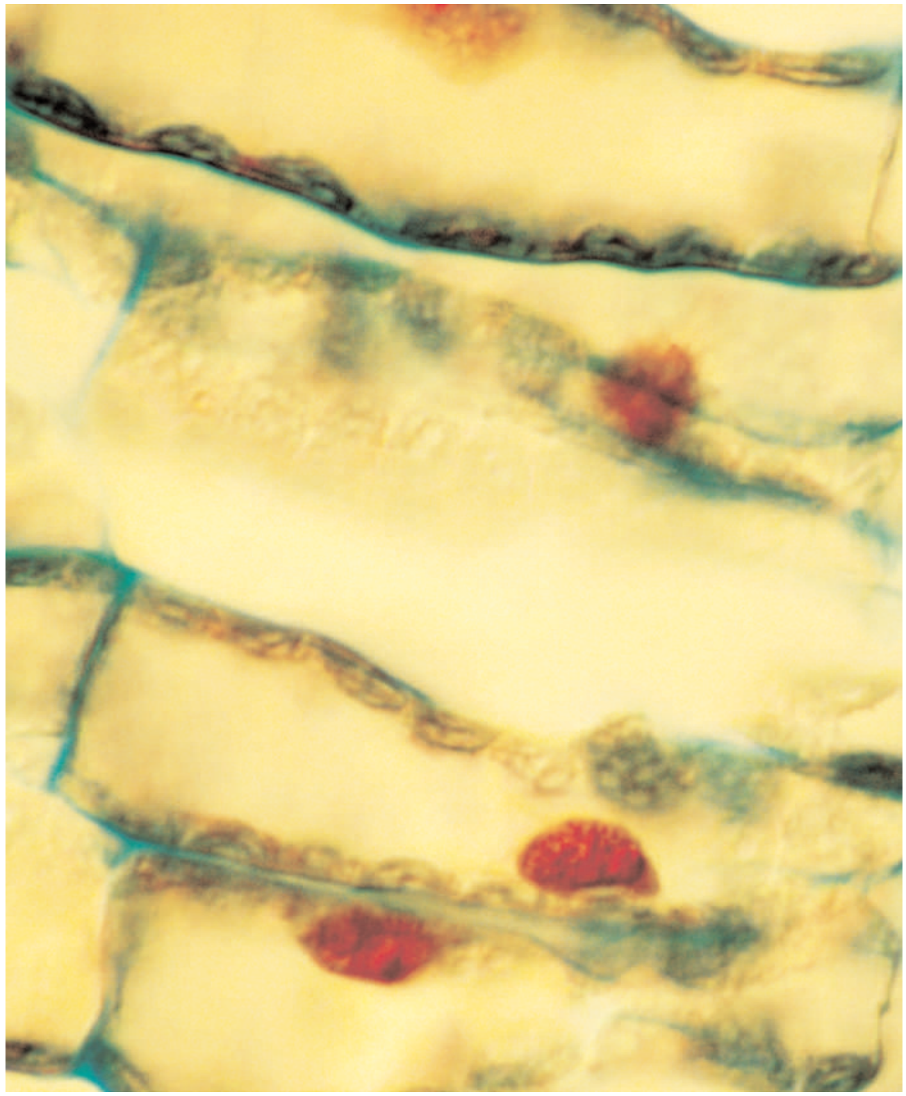
nonpolar not marked by separation of charge (unlike water and other polar substances)

hydrophobic water repellent

enzyme a protein that controls a reaction in a cell

All plant cell membranes share the same basic structure but differ in the makeup of specific components. All membranes also share the important property of semi-impermeability. Small molecules such as water move readily across the membrane, but larger molecules can move only if the appropriate integral proteins are present.

Nucleus. The nucleus is the most prominent structure within the protoplast and contains the genetic information responsible for regulating cell metabolism, growth, and differentiation. The nucleus contains the complex of deoxyribonucleic acid (DNA) and associated proteins, known as chromatin in the uncondensed state and as chromosomes in the condensed state. The chromatin is embedded in a clear matrix called the nucleoplasm. Nuclei also contain a densely granular region, called the nucleolus, that is the site of ribosome synthesis. The nucleus is bounded by a double membrane, the nuclear envelope. The two membranes of the nuclear envelope are joined at sites called nuclear pores. Each nuclear pore is an elaborate structure that allows macromolecules such as ribo-



A micrograph of the nuclei of plant cells.

somal subunits and ribonucleic acid (RNA) to pass between the nucleus and the cytoplasm.

Endomembrane System. The cytoplasm of plant cells has a continuous network of internal membranes called the endomembrane system. The nuclear envelope forms part of this system and is continuous with another component, the endoplasmic reticulum (ER). The ER consists of flattened sacs or tubes known as **cisternae**. There are two types of ER, smooth and rough, that are interconnected but carry out different functions. Rough ER tends to be lamellar (formed into flattened sacs) and is covered with ribosomes. Rough ER functions in protein synthesis and in the processing and storage of proteins made on the outer surface. In contrast, smooth ER tends to be tubular and is a major site of the synthesis of lipids such as those making up membranes.

cisterna a fluid-containing sac or space

dictyosome any one of membranous or vesicular structures making up the Golgi apparatus

vesicle a membrane-bound cell structure with specialized contents

Another major component of the endomembrane system is the Golgi apparatus (or **dictyosome**). The Golgi apparatus consists of a stack of flattened membrane cisternae and associated **vesicles**. The two primary functions of the Golgi apparatus are the modification of proteins synthesized on the rough

COMPARISON OF PLANT AND ANIMAL CELLS

Component	Plant Cell	Animal Cell
Cell wall	Provides protection, support	Absent (some cells have extracellular matrix of protein)
Nucleus	Site of most of cell's genetic information	Site of most of cell's genetic information
Endoplasmic reticulum	Protein synthesis, processing, and storage, lipid synthesis	Protein synthesis, processing, and storage, lipid synthesis
Golgi apparatus	Protein processing, secretion	Protein processing, secretion
Vacuole	Provides turgor storage	Absent
Mitochondrion	Cellular respiration	Cellular respiration
Plastid	Photosynthesis, color, starch or lipid storage	Absent
Peroxisome	Oxidizes fatty acids, photorespiration in green tissues	Oxidizes fatty acids
Cytoskeleton	Regulates cell shape, moves chromosomes, cytoplasmic streaming	Regulates cell shape, moves chromosomes, cytoplasmic streaming
Centriole	Absent	Required for nuclear division

ER and packaging of processed proteins and carbohydrates to be secreted outside the plasma membrane. The Golgi apparatus is a very dynamic part of cell structure. Vesicles carrying newly synthesized proteins or other precursors fuse with a cisterna on the forming face of the Golgi apparatus. As its contents are processed, a cisterna moves through the stack until it reaches the maturing face of the stack. Here the cisterna breaks up into separate vesicles that release their contents at the plasma membrane. Golgi apparatus are very numerous in secretory cells such as those of nectaries or root caps, and they also play a role in the secretion of cell wall matrix polysaccharides.

Vacuole. The vacuole is a conspicuous component of the cytoplasm in most plant cells. It may occupy more than 90 percent of cell volume in unspecialized parenchyma cells. The vacuole is surrounded by a membrane called the tonoplast that, because of the high density of integral proteins that are ion channels, plays an important role in the osmotic relationships of the cell. The vacuole stores a wide range of inorganic and organic substances such as the compounds that give beets their color (the water soluble red pigment anthocyanin), apples their sweetness (sucrose), lemons their sourness (citric acid), and tea its bitterness (tannin). In some plants, the vacuoles function as part of the plants' defense systems: it may be filled with sharp crystals of calcium oxalate that help deter **herbivores**.

herbivore an organism that feeds on plant parts

Chloroplast. Chloroplasts are organelles that function in photosynthesis and are another feature that distinguish plant from animal cells. Chloroplasts are bounded by a double membrane, the chloroplast envelope. The inner membrane of the envelope is invaginated (folded) to form flattened sacs within the chloroplast called thylakoids. Thylakoid membranes take two forms: stacks called grana, and sheets that connect the grana, called stroma thylakoids. Granal thylakoids contain photosynthetic pigments such as chlorophyll and carotenoids, as well as the proteins associated with the light reactions of photosynthesis. The carbon fixation reactions of photosynthesis take place within the amorphous portion of the chloroplast called the stroma. Chloroplast DNA is found in discrete regions within the stroma. The stroma also contains chloroplast ribosomes and other components required for protein synthesis. Therefore the chloroplast is semiautonomous, relying on the nuclear **genome** for only some of its proteins. Green chloro-

genome the genetic material of an organism

plasts are just one of several types of plastids that share the same basic structure. Chromoplasts are red or orange plastids that contain large amounts of carotenoid pigments and give fruits such as tomatoes and oranges their color. The brilliant colors of autumn leaves results from both the conversion of chloroplasts to chromoplasts and the formation of anthocyanin in the vacuole. Amyloplasts, such as those found in a potato tuber, are plastids that store starch.

Other Organelles. Mitochondria are small organelles with a double membrane that function in cellular respiration. The inner membrane of the mitochondrial envelope is infolded to form cristae that are the sites of the electron transfer system. The inner membrane encloses the matrix region, the location of the Krebs cycle. Like plastids, mitochondria possess their own DNA, ribosomes, and protein-synthesizing machinery. Proteins encoded by the mitochondria genome include ribosomal proteins and components of the electron transfer system.

Peroxisomes are small, single-membrane-bound organelles that function in photorespiration, a process that consumes oxygen and releases carbon dioxide. These peroxisomes are often found in association with chloroplasts in green leaf tissue. Other peroxisomes, called glyoxysomes, function in the conversion of stored fats to sucrose and are common in the tissues of germinating seeds.

filament a threadlike extension

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

contractile capable of contracting

Cytoskeleton. All living plant cells possess a cytoskeleton, a complex network of protein **filaments** that extends throughout the cytosol. The cytoskeleton functions in **mitosis**, cytokinesis, cell growth, and cell differentiation. The plant cell cytoskeleton has two major components: hollow cylinders called microtubules that are composed of tubulin protein, and solid microfilaments composed of actin protein. Microtubules guide chromosome movements during mitosis and the orientation of cellulose microfibrils during cell wall synthesis. The **contractile** microfilaments play a role in chromosome movement and in cytoplasmic streaming. SEE ALSO CARBOHYDRATES; CELL CYCLE; CELLS, SPECIALIZED TYPES; CELLULOSE; CELL WALLS; CHLOROPLASTS; PLASTIDS.

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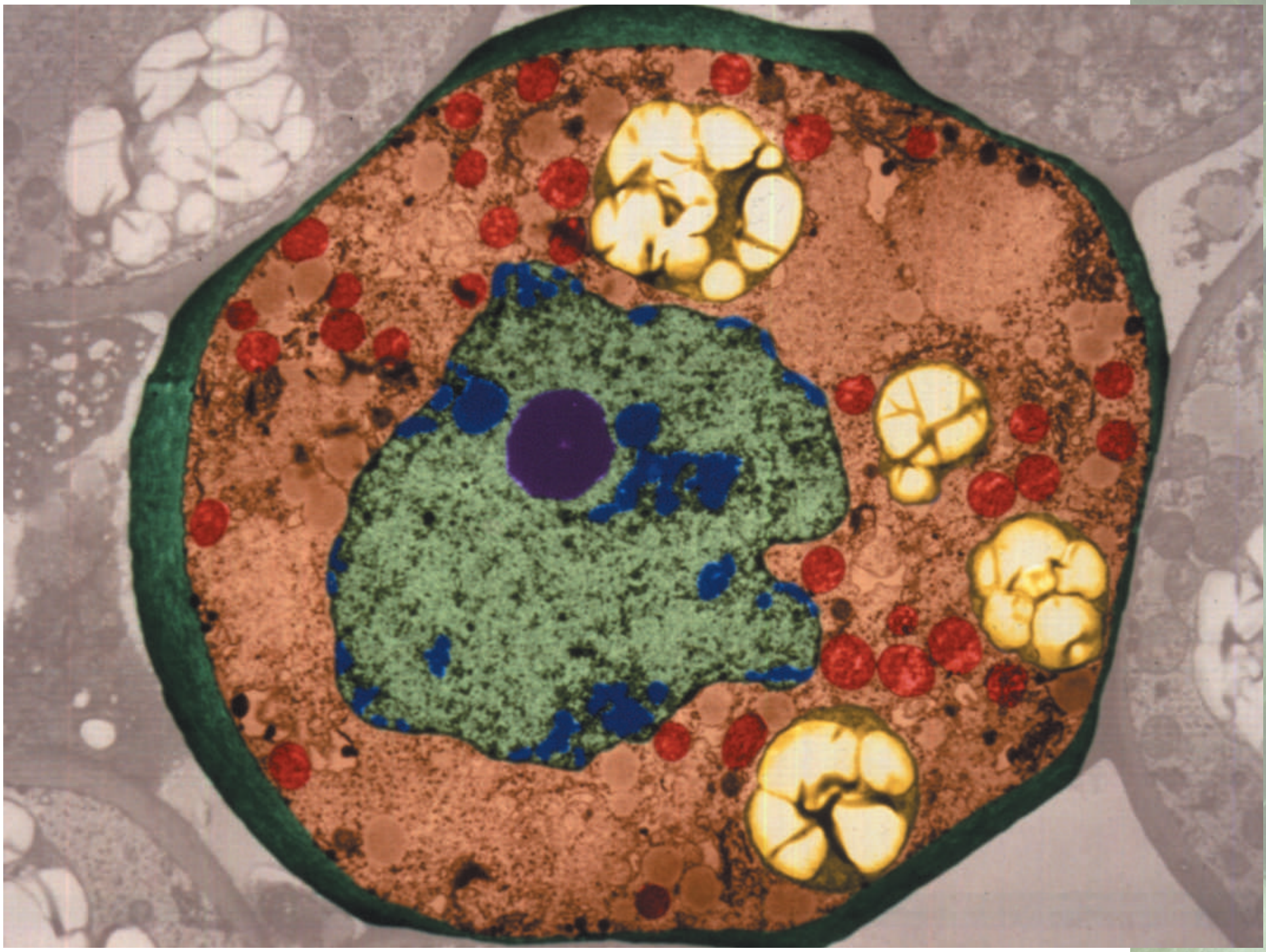
Cells, Specialized Types

vascular related to the transport of nutrients

The specialized cell types found in plant stems, leaves, roots, flowers, and fruits are organized into three tissue systems: the ground tissue system, the dermal tissue system, and the **vascular** tissue system. Each tissue system carries out a different general function: the vascular tissue system transports water and solutes over long distances within the plant, the dermal tissue system provides protection and gas exchange at the surface of the plant, and



Transmission electron micrograph of a parenchyma cell.

the ground tissue system provides cells that carry out photosynthesis, storage, and support. Each tissue system has many specialized cell types, and a few cell types are found in more than one tissue system.

The different types of specialized plant cells are distinguished by cell shape and by properties of the cell wall and **protoplast**. The plant cell wall is one of the most important distinguishing features of the different kinds of specialized cells. All plant cells have a thin and flexible primary wall, made of the **polymer** cellulose and other carbohydrates. Other cell types have, in addition to a primary wall, a thick, rigid secondary wall, made of cellulose impregnated with lignin.

protoplast the portion of the cell within the cell wall

polymer a large molecule made from many similar parts

Cells of the Ground Tissue System

Parenchyma cells are the generalized, multipurpose cells in the plant. Most parenchyma cells have thin primary walls and range from spherical to barrel-like in shape. Parenchyma cells often store food reserves, as in the starch-storing parenchyma cells of a potato tuber or the sugar-storing parenchyma cells of an apple. The parenchyma cells of green leaves are specialized for photosynthesis; these cells contain numerous large **chloroplasts** and are called chlorenchyma cells. Other parenchyma cells called transfer

chloroplast the photosynthetic organelle of plants and algae

solute a substance dissolved in a solution

nectaries organs in flowers that secrete nectar

cells are specialized for the transport of **solutes** across the cell membrane. These cells have a greatly enlarged surface area due to the highly convoluted inner surface of the cell wall. Transfer cells are found in **nectaries** where the extensive cell membrane houses transport channels that secrete sugars and other nectar components to the exterior of the cell.

Collenchyma cells function in the support of growing tissues. Individual collenchyma cells are long and narrow and have an unevenly thickened primary wall. Collenchyma cells form a long cable of thousands of cells that together can provide mechanical support while a stem or leaf elongates. Collenchyma is common in the veins of leaves and forms the strings of celery stalks.

Sclerenchyma cells function in the support of tissues that are no longer expanding. Individual sclerenchyma cells are long and narrow with a thick, hard, rigid secondary wall. Unlike parenchyma and collenchyma cells that are living cells, sclerenchyma cells are dead at maturity. The cell's function in mechanical support is carried out by the strong cell walls; a living protoplast is unnecessary. Sclerenchyma fibers make up the bulk of woody tissues and also form long strands in the leaves and stems of many plants. Natural fiber ropes such as those made from hemp or sisal plants are made up of thousands of sclerenchyma fibers. Some sclerenchyma cells called sclereids are much shorter than fibers; these form the hard layers of walnut shells and peach pits, and small clusters of sclereids form the grit in pear fruits.

Cells of the Dermal System

hydrophobic water repellent

transpiration movement of water from soil to atmosphere through a plant

Epidermal cells form the surface layer of the plant, the epidermis. Typical epidermal cells are flat and form a continuous sheet with no spaces between the cells. Each epidermal cell secretes a layer of the **hydrophobic** polymer cutin on the surface, which greatly reduces the amount of water lost by evaporation. Most epidermal cells also secrete waxes on the surface of the cutin, which further reduces **transpiration**, as well as wettability of the leaf surface. When you polish an apple, you are melting these surface waxes through friction. Epidermal cells of green leaves lack pigmented chloroplasts, allowing light to penetrate to the photosynthetic tissues within. Epidermal cells of petals often contain blue or red anthocynanin pigments within the vacuole or orange carotenoid pigments within the plastids, giving rise to the bright colors of many flowers.

Guard cells are specialized epidermal cells that function to open small pores in the plant surface, allowing the carbon dioxide needed for photosynthesis to diffuse from the external atmosphere into the chlorenchyma tissue. Guard cells are usually crescent-shaped, contain green chloroplasts, and are able to rapidly change their shape in response to changes in water status. As guard cells take up water, the pore opens; as they lose water the pore closes. The two guard cells and pore are termed a stomate.

herbivore plant eater

Trichomes are hairlike cells that project from the surface of the plant. They function to reduce water loss by evaporation by trapping water vapor near the plant surface. In some plants, trichomes are glandular and secrete sticky or toxic substances that repel insect **herbivores.**

Cells of the Vascular Tissue System

The vascular tissue system is composed of both xylem and phloem tissue. Xylem functions to carry water and mineral nutrients absorbed at the

A black-white colored concentration of cells on the epidermis of a plant showing plant stomata.

root tips throughout the plants roots, stems, and leaves. Vessel elements are the major cell type involved in the transport of water and these solutes. Vessel elements are elongate cells with thick secondary walls. Xylem sap travels under a negative pressure or vacuum, and the strong rigid walls keep the vessel elements from collapsing, much like the steel coil in a vacuum-cleaner hose. Like sclerenchyma fibers, vessel elements are dead at maturity, so that each cell forms an empty tube. Before vessel elements die, however, the cell's protoplast releases **enzymes** that degrade the cell wall at both ends of the cell, forming a perforation. Individual vessel elements are joined end to end at the perforations, thus forming a long, continuous pipe, the vessel. Other xylem cells called **tracheids** also function in transport of water and solutes, but are less efficient because they lack perforations and do not form long vessels. Xylem tissue also contains sclerenchyma cells that function in support and parenchyma cells that function in storage or as transfer cells. When transfer cells are found in the xylem, they function to recover valuable solutes such as nitrogen compounds from the sap traveling in the xylem vessels.

enzyme a protein that controls a reaction in a cell

tracheid a type of cell that conducts water from root to shoot

Phloem tissue functions to transport the products of photosynthesis from green tissues to parts of the plant where energy-rich carbohydrates are required for storage or growth (a process called translocation). Sieve elements are the conducting cells of the phloem. Sieve elements are elongated cells, with a thick primary wall. Phloem sap travels under a positive pressure, and the thick, elastic cell walls allow the cells to adjust to the fluctuations in pressure over a day-night cycle. Sieve elements have large, conspicuous pores on the end walls, forming a sieve plate. The sieve plate pores allow the phloem sap to travel from cell to cell along the file of cells called a sieve tube. Each sieve element is living, with an intact plasma membrane; the differential permeability of the membrane prevents solutes from leaking out of the sieve tube. Sieve-tube elements lack a nucleus and some other components of the cytoplasm; this feature functions to keep the pores unplugged. Companion cells are small parenchyma cells associated with each sieve element. The nucleus of the companion cell must direct the metabolism of both the companion cell itself and of its sister sieve element. SEE ALSO ANATOMY OF PLANTS; CELL CYCLE; CELLS; FIBER AND FIBER PRODUCTS; TISSUES; TRANSLOCATION; TRICHOMES; VASCULAR TISSUES; WATER MOVEMENT.

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Cellulose

polysaccharide a linked chain of many sugar molecules

nanometer one-millionth of a meter

turgor the internal pressure pushing outward in a plant cell

Cellulose is a major structural component of the cell walls of all land plants, including trees, shrubs, and herbaceous plants. The cell wall is a complex **polysaccharide** layer that surrounds each cell within a plant. Chemically, cellulose is a polysaccharide made up of long, unbranched chains of glucose linked end to end, making a very flat chain. (Starch is also made up of glucose, but linked such that it curls, resulting in very different properties.) Many cellulose chains associate side by side to make a cellulose ribbon, or microfibril, that has exceptional mechanical strength and chemical stability. Cellulose microfibrils, which are approximately 5 to 10 **nanometers** thick and many micrometers long, make cell walls strong and able to resist large forces, such as those generated internally by **turgor** pressure or externally by the weight of the plant or by wind. Economically, cellulose is important as a major component of wood products and of fibers used to make paper and textiles, such as cotton and linen. For industry, cellulose is dissolved and spun as a thread (called rayon) or formed into a thin sheet (cellophane). Cellulose is also chemically modified to make many kinds of films (such as cellulose acetate), thickeners used in foods and paints, and coatings such as nail polish (which contains cellulose nitrate). SEE ALSO CARBOHYDRATES; CELL WALLS; FIBER AND FIBER PRODUCTS.

Daniel Cosgrove

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Cell Walls

With a few notable exceptions, plant cells are encased in a complex **polymeric** wall that is synthesized and assembled by the cell during its growth and differentiation. Cell walls function as the major mechanical restraint that determines plant cell size and **morphology**. They enable cells to generate high **turgor** pressure and thus are important for the water relations of plants. Cell walls also act as a physical and chemical barrier to slow the invasion of bacteria, fungi, and other plant pests, and they also take part in a sophisticated signaling and defense system that helps plants sense **pathogen** invasion by detecting breakdown products from wall **polysaccharides.** Finally, cell walls glue plant cells together and provide the mechanical support necessary for large structures (the largest trees may reach 100 meters in height, generating tremendous compression forces due to their own weight).

polymer a large molecule made from many similar parts

morphology shape and form

turgor the internal pressure pushing outward in a plant cell

pathogen disease-causing organism

polysaccharide a linked chain of many sugar molecules

Cell walls vary greatly in appearance, composition, and physical properties. In growing cells, such as those found in shoot and root **apical meristems**, cell walls are pliant and extensible (that is, they can extend in response to the expansive forces generated by cell turgor pressure). Such walls are called primary cell walls. After cells cease growth, they sometimes continue to synthesize one or more additional cell wall layers that are referred to as the secondary cell wall. Secondary cell walls are generally inextensible and may be thick and **lignified**, as in the xylem cells that make up wood.

apical at the tip

meristem the growing tip of a plant

lignified composed of lignin, a tough and resistant plant compound

Composition and Molecular Architecture

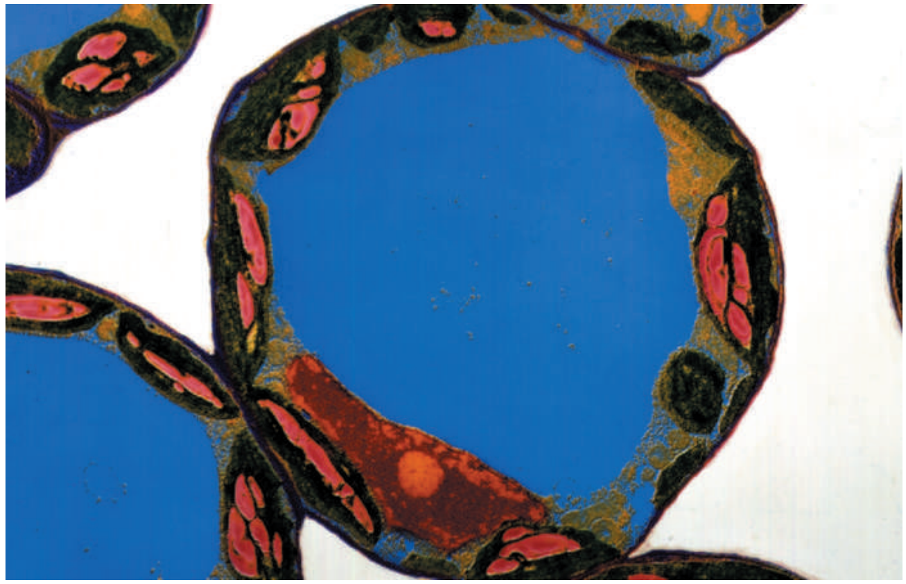
The primary cell wall contains three major classes of polysaccharides: cellulose, hemicellulose, and pectin. Hemicellulose and pectin collectively constitute the matrix polysaccharides of the cell wall. Cellulose is present in the form of thin microfibrils, about 5 **nanometers** in thickness and indefinite length. The cellulose microfibril is made up of many parallel chains of 1,4-β-glucan, which is a linear polymer of glucose molecules linked end-to-end through the carbon atoms numbered 1 and 4. These chains form a crystalline ribbon that makes cellulose very strong and relatively **inert** and indigestible.

nanometer one-millionth of a meter

inert incapable of reaction

Hemicellulose refers to various polysaccharides that are tightly associated with the surface of the cellulose microfibril. They are chemically similar to cellulose, except they contain short side branches or kinks that prevent close packing into a microfibril. The backbone of hemicelluloses is typically made up of long chains of glucose or xylose residues linked end to end, often ornamented with short side chains. The most abundant hemicelluloses are xyloglucans and xylans. By adhering to the surface of cellulose microfibrils, hemicelluloses prevent direct contact between microfibrils, but may link them together in a cohesive network.

Pectin constitutes the third class of wall polysaccharide. It forms a gel-like phase in between the cellulose microfibrils. Unlike cellulose and hemi-



Colored transmission electron micrograph of cells in a young leaf.

cellulose, pectin may be solubilized with relatively mild treatments such as boiling water or mildly acidic solutions. Pectin includes relatively simple polysaccharides such as polygalacturonic acid, a long chain of the acidic sugar galacturonic acid. This pectin readily forms gels in which calcium ions link adjacent chains together. Other pectin polysaccharides are more complex, with backbones made of alternating sugar residues such as galacturonic acid and rhamnose, and long side chains made up of other sugars such as arabinose or galactose. In the cell wall, pectins probably form very large aggregates of indefinite size.

In addition to these polysaccharides, primary cell walls also contain a small amount of structural proteins, such as hydroxyproline-rich glycoproteins and glycine-rich proteins.

Secondary cell walls are like primary walls except they contain more cellulose and less pectin than primary walls, and often contain hemicellulose polymers of differing composition. Many, but not all, secondary walls also contain lignin, which is a complex and irregular phenolic polymer that acts like epoxy to glue the wall polysaccharides together. Lignification greatly increases the mechanical strength of cell walls and makes them highly resistant to degradation.

Cell Wall Synthesis

The components of the cell wall are synthesized via distinct pathways and then assembled at the cell surface. Cellulose is synthesized by a large, cellulose synthase **enzyme** complex embedded in the plasma membrane. This complex is large enough to be seen in the electronic microscope and looks like a hexagonal array, called a particle rosette because of its appearance. The cellulose-synthesizing complex synthesizes thirty to forty glucan chains in parallel, using **substrates** from the cytoplasm. The growing chains are extruded to the outside of the cell via a pore in the complex and the chains then crystallize into a microfibril at the surface of the cell. In some algae the cellulose synthase complexes assume other configurations and this

enzyme a protein that controls a reaction in a cell

substrate molecules acted on by enzymes is associated with differing sizes and structures of the microfibril. Genes encoding plant cellulose synthases were first identified in the late 1990s, and the molecular details of how these proteins synthesize cellulose is still being studied.

The matrix polysaccharides (hemicellulose and pectin) are synthesized in the Golgi apparatus by enzymes called glycosyl transferases. They are transported to the cell wall via **vesicles** that fuse with the plasma membrane and dump their contents into the wall space. The matrix polymers and newly extruded cellulose microfibrils then assemble into an organized cell wall, probably by spontaneous self-organization between the different classes of polymers.

vesicle a membrane-bound cell structure with specialized contents

Wall enzymes may also aid assembly by forming cross-links between wall components. For example, some enzymes remove side chains from the hemicelluloses. This enables the hemicelluloses to stick more readily to cellulose. Other enzymes cut and link polysaccharides together, forming a more intricate weave of matrix polysaccharides.

Economic Importance of the Cell Wall

The cell wall is unmatched in the diversity and versatility of its economic uses. Lumber, charcoal, and other wood products are obvious examples. Textiles such as cotton and linen are derived from the walls of unusually long and strong fiber cells. Paper is likewise a product of long fiber cell walls that are extracted, beaten, and dried as a uniform sheet. Cellulose can be dissolved and regenerated as a manmade fiber called rayon or in sheets called cellophane. Chemically modified cellulose is used to make plastics, membranes, coatings, adhesives, and thickeners found in a vast array of products, from photographic film to paint, nail polish to explosives. In agriculture, cell walls are important as animal fodder, whereas in the human diet, cell walls are important as dietary fiber or roughage. Pectin is used as a gelling agent in jellies, yogurt, low-fat margarines, and other foods, while powered cellulose is similarly used as a thickener in foods and as an inert filler in medicinal tablets. SEE ALSO Anatomy of Plants; Carbohydrates; Cells; Cellulose.

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Chaparral

Chaparral is an evergreen shrub vegetation that dominates the rocky slopes of southern and central California. It forms a nearly continuous cover of closely spaced shrubs 6 to 12 feet (2 to 4 meters) tall, with intertwining branches that make the vegetation nearly impenetrable to humans. Herbaceous vegetation (grasses and wildflowers) is generally lacking, except after fires, which are frequent throughout the range. Because of complex patterns

Montane chaparral vegetation such as xerophytic shrubs and singleleaf piñon (*Pinus monophylla*) can survive the seasonal droughts that occur on the flanks of the Sierra Nevadas.

topographic related to the shape or contours of the land

juxtaposition contrast brought on by closeness

alluvial plain broad area formed by the deposit of river sediment at its outlet

of **topographic**, soil, and climatic variations, chaparral may form a mosaic pattern in which patches of oak woodland, grassland, or coniferous forest appear in sharp **juxtaposition**. Fire frequency and soil are major factors that determine these patterns. Chaparral is replaced by grassland on frequently burned sites, especially along the more arid borders at low elevations (where shrub recovery is more precarious due to drought) and on deeper clay soils and **alluvial plains**, and by oak woodland on more moist slopes (where fires are less frequent and often less intense).

California chaparral is distributed in a region of Mediterranean climate, which has cool (40°F), wet winters and hot (95°F), dry summers. Rainfall is 10 to 20 inches (25 to 100 centimeters) annually, two-thirds of which falls November to April in storms of several days duration.

Plants of the Chapparal

The most widely distributed chaparral shrub is chamise (*Adenostoma fasciculatum*), an adapted shrub with short needlelike leaves, which is distributed from Baja California in the south to Oregon in the north. Buckbrush (*Cean-*

othus spp.) and manzanitas (*Arctostaphylos*) are large **genera** (about seventy species each) and often form pure stands commonly referred to as manzanita chaparral or ceanothus chaparral. Some species are highly restricted in distribution, whereas others are nearly as widespread as chamise. Most species in these two genera are **endemic** to the California chaparral and have suites of characters reflecting a long association with fire. For example, many species of *Ceanothus* and *Arctostaphylos* have woody tubers at their base that sprout new stems after fire. All species in these two genera produce deeply **dormant** seeds that accumulate in the soil and require fire for germination.

genera plural of genus

endemic belonging or native to a particular area or country

dormant inactive, not growing

At the lowest elevations throughout much of its range, chaparral is commonly replaced by a smaller and highly aromatic vegetation known as soft chaparral or coastal sage. This vegetation differs from chaparral by being summer-deciduous; this loss of leaves during drought confers a greater ability to tolerate the drier conditions at low elevations. The dominant shrubs are only 3 to 6 feet (1 to 2 meters) tall and include California sagebrush (*Artemisia californica*), black sage (*Salvia mellifera*), California buckwheat (*Eriogonum fasciculatum*), deerweed (*Lotus scoparius*), and monkeyflower (*Mimulus aurantiacus*). These smaller shrubs grow rapidly and have well-developed wind dispersal of seeds so they often **colonize** disturbed sites.

colonize to inhabit a new area

The Californian Mediterranean climate is conducive to massive wildfires. Mild, wet winters contribute to a prolonged growing season, which, coupled with moderately fertile soils, result in dense stands of contiguous fuels. Long summer droughts produce highly flammable fuels that are readily ignited by lightning from occasional thunderstorms but more commonly as the result of human carelessness. On average fire frequency for any one area is about every two to three decades, but this may be more frequent than in the past. Throughout much of its range, chaparral forms a continuous cover over great distances, and as a result, huge wildfires that cover tens of thousands of acres are common, particularly during Santa Ana wind conditions. These dry winds from the east occur every autumn and often exceed sixty miles per hour. Some scientists have suggested that massive wildfires are an artifact due to modern-day fire suppression, which causes an unnaturally heavy accumulation of plant fuel. Others dispute this conclusion, pointing to evidence that shows this vegetation has always experienced large, high-intensity fires.

The Role of Fire

Although shrubs dominate chaparral, the **community** comprises a rich diversity of growth forms, many of which are conspicuous only after fire. In addition to evergreen shrubs and trees, there are semi-deciduous subshrubs, slightly ligneous (hardened) **suffrutescents**, woody and herbaceous vines, and a rich variety of herbaceous perennials and annuals. A large number of these species arise from dormant seeds deposited into the soil decades earlier, following an earlier fire. Dormancy is broken in some seeds by heat but in many other species smoke from the fire triggers germination. In the first spring following fire, there is an abundant growth of herbaceous plants, which are relatively short-lived and are replaced by shrubs within the first five years. The postfire herbaceous flora often is dominated by annual species that live for less than one year, and species diversity is typically greatest in this first year after fire. Recovery of shrub **biomass** is from basal resprouts and seedling recruitment from a dormant soil-stored seed bank.

community a group of organisms of different species living in a region

suffrutescent a shrub-like plant with a woody base

biomass the total dry weight of an organism or group of organisms

The striking contrast between the diminished herb growth under mature chaparral and the flush of herbs after fire is thought to be caused by allelopathic (chemical) suppression of germination by the overstory shrubs. Many of the smaller shrubs, such as sage (*Salvia* spp.) or sagebrush (*Artemisia* spp.), release volatile, aromatic **compounds**, and it has been suggested that these compounds inhibit the growth of competing grasses and wildflowers. This theory holds that fire destroys these **toxins**, and that this occurs throughout the shrub land and in a zone at the border between shrub lands and grasslands, forming a meter-wide strip known as the bare zone. However, experiments in which animals have been excluded from the bare zone demonstrate that the lack of herbaceous plants in and around mature shrub lands is as much due to animal **predation** as it is to chemical inhibition. In addition, it appears that the vast majority of species that germinate after fire do so more because their dormant seeds are stimulated to germinate by fire.

compound a substance formed from two or more elements

toxin a poisonous substance

predation the act of preying upon; consuming for food

Resource agencies often respond to wildfires with emergency revegetation programs, which drop grass seed on newly burned sites with the expectation that this will reduce soil erosion and eliminate the threat of mudslides and flooding. The rationale for this management is that burned sites have greatly increased surface flow of rainwater and thus high soil erosion. Emergency seeding is considered essential on sites following exceptionally intense fires because of the anticipated negative effects. Throughout the state of California the seed of choice has been the nonnative annual ryegrass (*Lolium multiflorum*). However, there is abundant evidence that this practice fails to substantially reduce threats of mudslides and flooding and competitively displaces the native flora.

Some scientists have suggested that chaparral shrub lands become **senescent** if they are free of fire for more than a few decades. Detailed studies, however, find that these shrub land **ecosystems** can retain productive vegetation for a century or more, and in fact some shrubs require long periods without fire for successful seedling recruitment. SEE ALSO ALLELOPATHY; BIOME; ECOLOGY, FIRE.

senescent aging or dying

ecosystem an ecological community together with its environment

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Chestnut Blight

The American chestnut (*Castanea dentata*) formerly was the most prevalent tree in the mountains of the eastern United States, comprising more than 25 percent of the forest. Chestnut was a fast growing, valuable tree. Its wood was used in all phases of construction, from rough timbers and telephone poles to fine furniture; its bark was a source of **tannins** for making leather; and its nuts provided nourishment for wildlife, livestock, and people.

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

The chestnut blight fungus (*Cryphonectria parasitica*) was introduced into North America at the beginning of the twentieth century, probably on imported Japanese chestnut seedlings. The blight fungus swept through the chestnut forests, killing approximately ten billion trees by the middle of the century. Fewer than one hundred trees within the original range survived the onslaught of blight. This level of destruction of an entire, well-established species by a disease is unparalleled in the annals of plant and animal pathology.

The blight fungus kills chestnut trees by destroying the phloem and outer layers of xylem, growing around the tree trunk at a rate of approximately 15 centimeters per year. When all the bark and underlying wood around a trunk is killed, the tree dies because it can no longer circulate water and sugar between its leaves and roots.

Millions of chestnut sprouts persist today in the Appalachian Mountains, escaping blight due to their small size (although they are still susceptible to the disease). These are being used as mother trees in an effort to backcross the blight resistance of the Chinese chestnut tree into its American cousin. Scientists also have found some viruses that attack the blight fungus, making it unable to kill trees. It is hoped that one or both of these approaches will allow the return of this noble tree. SEE ALSO INTERACTIONS, PLANT-FUNGAL; PATHOGENS.

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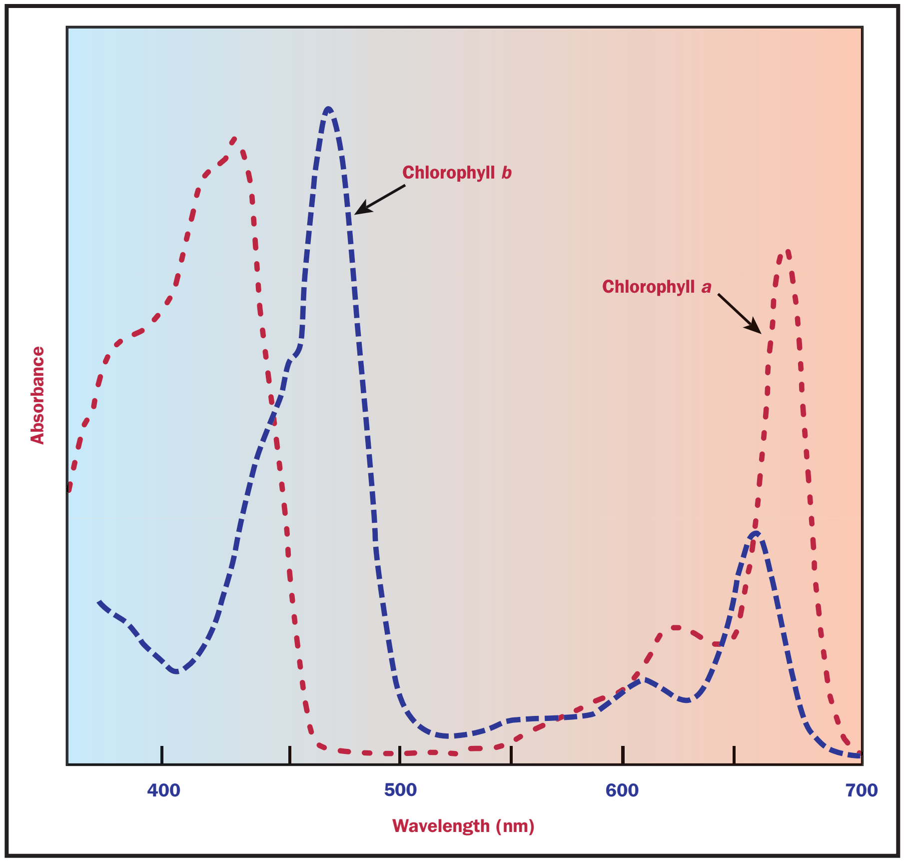
Chlorophyll

All forms of life on the surface of Earth are powered, directly or indirectly, by absorption of the energy in sunlight by chlorophyll molecules in plant cells. The subsequent processes of photosynthesis convert light energy to

The absorption spectra of chlorophyll *a* and *b* in methanol.



reaction center a protein complex that uses light energy to create a stable charge separation by transferring a single electron energetically uphill from a donor molecule to an acceptor molecule, both of which are located in the reaction center

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

chloroplast the photosynthetic organelle of plants and algae

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

nanometer one-millionth of a meter

enzyme a protein that controls a reaction in a cell

electrical and then chemical energy, which the cell uses for growth. The minimal absorption of green light by chlorophyll causes plants to have a green color (see accompanying graph).

Chlorophylls are cyclic tetrapyrroles, that is, molecules made by connecting four 5-membered pyrrole rings into a macrocycle. The initial biosynthetic precursor, 5-aminolevulinic acid (ALA), is made from the abundant amino acid glutamic acid. Condensation of two ALA molecules produces the 5-membered ring compound porphobilinogen. Four of these molecules are joined into a large ring structure, some of the side chains are modified, and the compound is oxidized to generate the fully conjugated double-bond arrangement that allows efficient absorption of light energy. At this stage, Mg^{2+} is inserted into the center of the large ring structure, and the fifth ring is formed.

The long hydrocarbon side chain causes chlorophyll to act as a lipid, allowing it to become embedded in thylakoid membranes. Chlorophyll *a* can be oxidized to chlorophyll *b*, which differs only in the presence of an aldehyde group on ring B. All chlorophyll molecules are bound to protein molecules and incorporated into complexes that allow energy absorbed by the molecules to be trapped in **reaction centers** of photosynthesis. In **eukaryotic** photosynthetic organisms, all these reactions occur in the **chloroplast**.

Other forms of chlorophyll also are found in nature. Some families of algae contain chlorophyll *c*, which does not have a long lipid tail and differs in several other respects. Chlorophyll *d*, which was found recently as the major chlorophyll in a photosynthetic **prokaryote** living inside ascidians in the Pacific Ocean, is similar to chlorophyll *b* but with the aldehyde on ring A. Bacteriochlorophylls, possibly the evolutionary ancestors of chlorophylls, occur in photosynthetic bacteria. Unlike other chlorophylls, bacteriochlorophylls absorb light in the infrared region, near 800 **nanometers** (nm). SEE ALSO CHLOROPLASTS; PHOTOSYNTHESIS, LIGHT REACTIONS AND; PIGMENTS.

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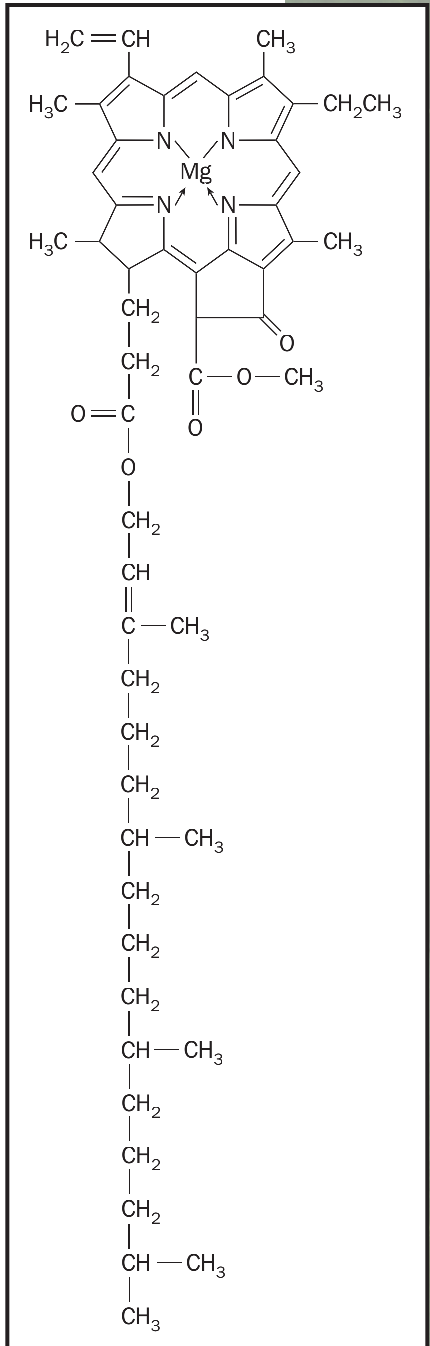
Chloroplasts

The chloroplast is a membrane-bound organelle within a cell that conducts photosynthesis. From the molecular perspective, the chloroplast is very large and contains millions of protein molecules along with vast sheets of membranes. If we imagine an average-sized **enzyme** molecule to be the size of an automobile, a chloroplast in a plant leaf cell would be about 6 kilometers on its long axis and about 2 kilometers on its short axis. The approximately cube-shaped plant cell, 15 to 20 kilometers per side, would contain fifty to one hundred of these compartments.



Structure of chlorophyll *a*.

Structure of Chloroplasts

The chloroplast is enclosed by two membranes, designated the outer and inner membranes of the chloroplast envelope. About one-half the volume within the chloroplast is occupied by stacks of fifty to one hundred flattened sacs called thylakoids, from the Greek word meaning "like an empty pouch." The thylakoid membrane surrounds the lumen or interior space and is the major membrane of the chloroplast. Groups of thylakoids adhere into stacks called grana. The remaining soluble phase of the chloroplast, outside thylakoids, is the stroma.

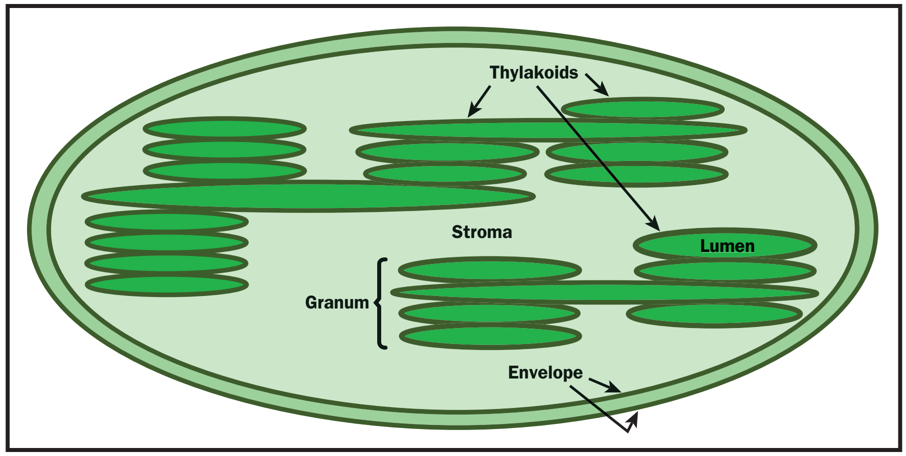
Function of Chloroplasts

The primary function of chloroplasts is photosynthesis, the light-driven fixation of carbon dioxide into organic **compounds**. The products of the photochemical reactions that occur within thylakoid membranes provide the material with which the plant cells grow and on which all forms of life on the surface of Earth depend.

Photosynthesis begins when light is absorbed by the green pigment chlorophyll, which occurs only in photosynthetic thylakoid membranes. The absorbed light energy is transferred to a **reaction center** called Photosystem II (PSII), where electrons are removed from water to release molecular oxygen. The electrons are carried through an electron transport chain in thylakoid membranes to Photosystem I (PSI) to eventually produce reduced compounds (for example, **NADPH**) that drive carbon fixation reactions. The flow of electrons through this linked set of carriers also transfers protons (H^+) from the stroma to the thylakoid lumen, which generates a concentration gradient. These protons can only flow back to the stroma through protein channels within the thylakoid membrane. At the stromal

compounds substances formed from two or more elements

NADPH reduced form of nicotinomide adenine dinucleotide phosphate, a small, water-soluble molecule that acts as a hydrogen carrier in biochemical reactions



Major structural compartments of a plant cell chloroplast.

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

end of the membrane channels is adenosine triphosphate (**ATP**) synthase, which uses the flow of H^+ to drive the synthesis of H^+ ATP. ATP is used as the primary energy source for biosynthetic reactions within the cell. The ATP and NADPH created are then used to produce sugars from carbon dioxide.

The most abundant enzyme in the biosphere, ribulose 1,5-bisphosphate carboxylase/oxygenase (rubisco, for short), catalyzes the reaction of carbon dioxide with ribulose 1,5-bisphosphate, a 5-carbon compound, to make glyceraldehyde 3-phosphate and 3-phosphoglycerate. These two 3-carbon compounds enter the reductive pentose-phosphate cycle (also called the Calvin-Benson cycle) and eventually are converted to a 6-carbon sugar, glucose 6-phosphate, the ultimate product. Glucose 6-phosphate is the precursor of many of the storage products in the plant cell, such as starch, sucrose, and lipids, and is also the starting point for biosynthesis of most of the cellular material. All fatty acids and most amino acids used by the cell are also synthesized in the chloroplast.

saturate containing as much dissolved substance as possible

Rubisco is a large enzyme—containing eight large (molecular weight 52,000) and eight small (molecular weight 14,000) subunits—that is also very sluggish, catalyzing a reaction only three times per second even when **saturated** with carbon dioxide. The usual concentration of carbon dioxide in the watery cell interior is sufficient for only one-half this rate. Perhaps these are the reasons why plants developed mechanisms to achieve a high concentration of the enzyme in the stroma to catalyze this reaction that is essential to maintenance of life. Approximately two million molecules of rubisco are present in each chloroplast.

Development of Chloroplasts

vesicle a membrane-bound cell structure with specialized contents

Germination of a seed results in growth of a shoot, in which the initial plastids exist with the cells as simple, double-membrane-enclosed **vesicles** that contain deoxyribonucleic acid (DNA), ribosomes, and a set of enzymes needed for expression of the DNA. These structures, only about 20 percent of the size of a mature chloroplast, are called proplastids. When the shoot reaches the light, the plastid begins the synthesis of chlorophyll, which is required for nearly all remaining aspects of development. Synthesis of lipids, which form the framework of thylakoid membranes, is stimulated within the inner membrane of the envelope.

Proteins are also imported into the chloroplasts after synthesis on cytosolic ribosomes as precursor molecules. Such proteins contain an extension at their amino-terminal end, designated the transit sequence, that serves as a targeting signal for import into the chloroplast. As soon as the protein reaches the stroma, the transit sequence is removed by a specific protease. The chloroplast envelope contains an elaborate apparatus made of numerous protein molecules that function to guide proteins through the membranes into the interior. While some proteins remain embedded in the membrane, others pass through the envelope into the stroma. Of these, a relative few are also transported across thylakoid membranes into the thylakoid lumen. The two major proteins that are imported are the precursor of the small subunit of rubisco, which is released into the stroma, and the chlorophyll-binding proteins, which are integrated into large light-harvesting antenna complexes within the envelope inner membrane. These complexes absorb and funnel light energy to reaction centers to drive the light reactions of photosynthesis. The addition of lipids, pigments, and proteins causes expansion of this membrane, which pinches off into vesicles that subsequently fuse to construct the large thylakoid structure in the interior of the organelle.

Chloroplasts grow and divide along with the cell they reside in as the plant grows. Nearly one hundred copies of the chloroplast **genome**, a circular, rather small molecule of DNA, are present in each chloroplast. The genes are expressed by transcription to make messenger ribonucleic acid

genome the genetic material of an organism

False color transmission electron micrograph of a developing chloroplast in a tobacco leaf.

(mRNA), which is translated on chloroplast ribosomes. These ribosomes, about one million in total number per chloroplast, are synthesized inside the chloroplast and are slightly smaller than the cytosolic ribosomes that are encoded by nuclear DNA. Therefore, chloroplasts are able to synthesize their own proteins, but in fact make only about 10 percent of the proteins they contain. Although a chloroplast may contain 500 to 1,000 different proteins, the chloroplast genome contains only 70 to 80 genes for proteins among its total of about 150 genes. The remainder of the proteins are encoded in nuclear DNA and imported.

Evolution of Chloroplasts

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

eukaryotic a cell with a nucleus (*eu* means “true” and *karyo* means “nucleus”); includes protists, plants, animals, and fungi

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

The presence of a separate genome, along with similarities between the structures of the chloroplast and photosynthetic **cyanobacteria**, prompted scientists to propose that chloroplasts originated as the result of an early **eukaryotic** cell engulfing a **prokaryotic** cyanobacterium. This proposal has recently received nearly unequivocal support in view of the remarkable similarities in sequences in genes that occur within chloroplasts and cyanobacteria. The evidence suggests that this event, called endosymbiosis, happened once, or a few times, about one billion years ago and that chloroplasts in all photosynthetic eukaryotic organisms are descendants of this event. Shortly after the cyanobacterium became resident within the host cell, much of the genetic information in the bacterium was transferred to the nucleus of the host. Following this endosymbiosis event, as photosynthetic organisms evolved, their chloroplasts diverged as well.

diatoms hard-shelled single-celled marine organisms; a type of algae

The divergent evolutionary heritages of chloroplasts in various organisms has led to a collection of unique properties. Most of the variety occurs among the algae. Light-harvesting complexes in green algae (Chlorophyceae) contain chlorophylls *a* and *b* bound to proteins within the membrane that are very similar to higher plants. The red algae (Rhodophyceae) are similar to green algae except that they contain phycobilisomes as major light-harvesting complexes attached to the surface of thylakoid membranes and do not contain chlorophyll *b*, which is similar to cyanobacteria. Brown algae (Phaeophyceae), yellow-green algae (Chrysophyceae), **diatoms** (Bacillariophyceae), and dinoflagellates (Dinophyceae) contain proteins similar to those in light-harvesting complexes in green algae; they differ in that they contain chlorophyll *c* instead of chlorophyll *b*. These latter algal families contain an additional pair of membranes surrounding the chloroplast. These extra membranes are thought to have originated when a second eukaryotic cell engulfed an entire chloroplast-containing eukaryotic alga. SEE ALSO Cells; Chlorophyll; Endosymbiosis; Photosynthesis, Carbon Fixation and; Photosynthesis, Light Reactions and; Plastids.

J. Kenneth Hoober

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Chocolate *See Cacao.*

Chromosomes

The genetic material in plants, animals, and fungi is called deoxyribonucleic acid (DNA), a long, linear **polymer** that is physically organized at the microscopic level into chromosomes. Chromosomes are threadlike cellular structures made up of elaborately packaged DNA complexed with proteins. When a cell reproduces itself to make two identical daughter cells, the chromosomes are replicated and divided so that each daughter cell has the same genetic and DNA content. The chromosome division process is called mitosis. During mitosis the individual chromosomes can be stained and seen under a microscope.

polymer a large molecule made from many similar parts

Genes code for the production of structural proteins and **enzymes** and are located at specific sites along the DNA. These sites are called loci (singular: locus) and represent a sort of chromosomal street address for the basic units of heredity, the genes. Genetic loci number in the tens of thousands for most plant species, and they are physically linked if they reside on the same chromosome.

enzyme a protein that controls a reaction in a cell

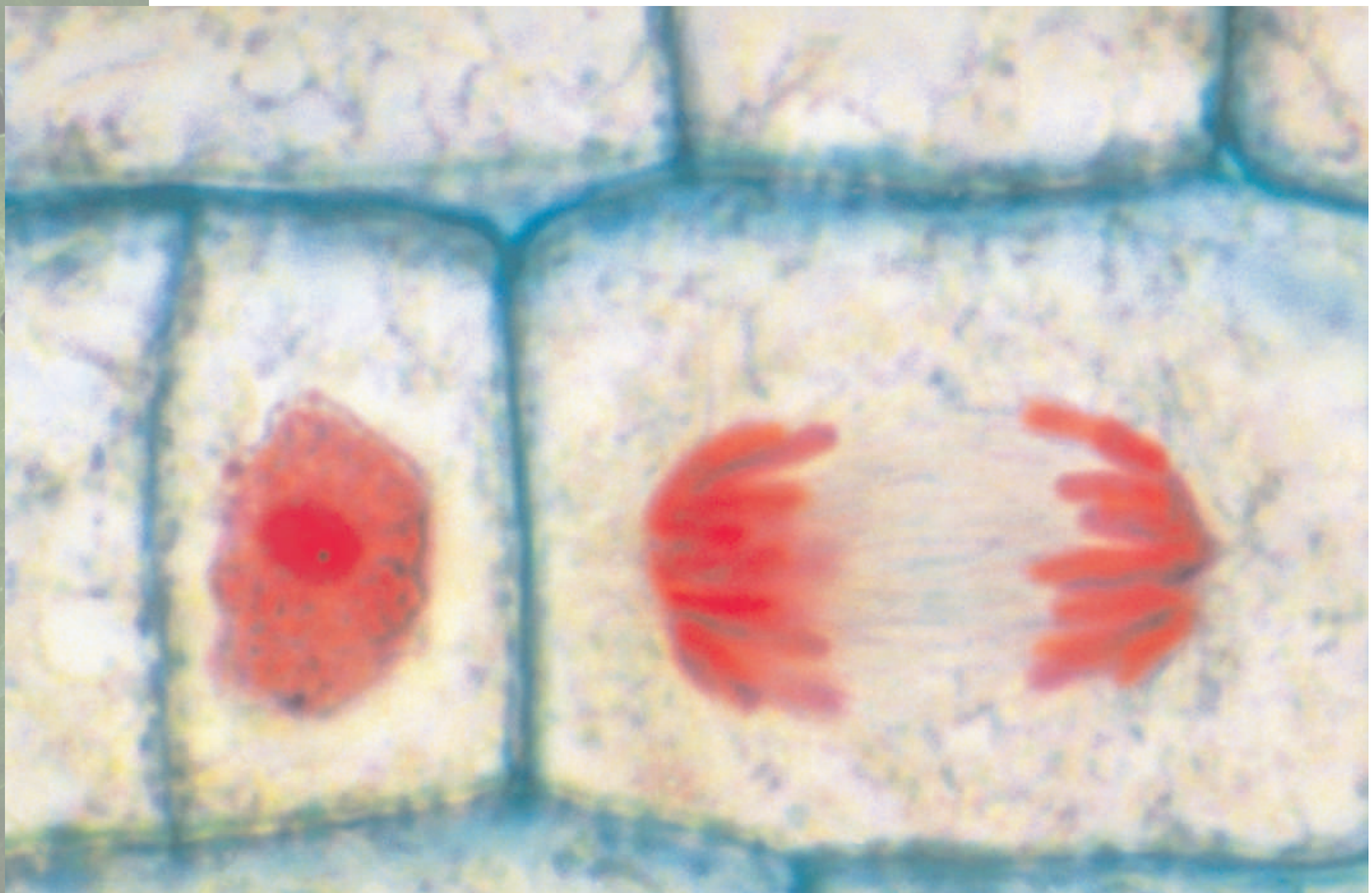
Plant chromosomes replicate and divide in a typical fashion. They are also subject to a type of molecular infection by small, self-replicating, or mobile, pieces of DNA called transposable DNA elements (or transposons), which can hop from one chromosome to another, as described below.

Historically, some important basic principles of genetics and heredity have come from the scientific study of plants. In his classic work on the transmission of traits (such as wrinkled seed) in peas, Gregor Mendel discovered the basic rules of heredity. Mendel showed that both mother (egg) and father (pollen sperm) contribute genetic factors to the next generation by cell union at fertilization. Similarly, the discovery of the existence of jumping genes (described below) was made by Barbara McClintock in her work on corn (*Zea mays*).

Plant chromosome research has come full circle in the new millenium with the ability to relate molecular structure to whole plant function. For instance, the wrinkled seed trait studied by Mendel was recently discovered to have been caused by a transposon that hopped into and broke a gene involved in filling the pea seed with starch. Mendel was able to track the broken gene through multiple generations by observing the inheritance of the wrinkled seed trait. Understanding plant chromosome structure and function helps bridge the gap between molecular biology and whole plant biology.

Physical Description

DNA does not exist in the cell as an isolated chemical, but rather as an elaborately packaged and microscopically visible structure called a chromosome. All chromosomes are comprised of both DNA and proteins, although only the DNA contains the genetic code. Each chromosome carries thousands of genes, and each time a cell divides all of the cell's chromosomes are replicated, divided, and sorted into two pools, one for each new daugh-



The anaphase stage of mitosis in the cell of an allium root. The chromosomes, replicated and condensed into chromatids, are lined up along an axis.

ter cell. Each chromosome has a centromere (the site on the chromosome where the spindle attaches), which functions as a "luggage handle" for the genetic cargo. This attachment provides the mechanical basis for movement of chromosomes toward one of the two pointed ends (poles) of the football-shaped spindle apparatus.

The entire complement of chromosomes in a given cell or for a given species is referred to as the genome. Plant genomes vary in total DNA content from one species to the next, yet they all have a similar number of functional genes (between fifty and one hundred thousand per individual) required to support the life cycle of a typical plant.

Chromosome Pairing and Segregation

Because most plant species reproduce sexually, they have genomes consisting of two complete sets of genetic instructions, one from each parent, just like humanoids. Most cells of the plant body (stems, roots, leaves) carry this duplicate set, which makes them **diploid**.

diploid having two sets of chromosomes, versus having one (haploid)

haploid having one set of chromosomes, versus having two (diploid)

During meiosis, the genome content gets reduced to one complete set of chromosomes per cell, producing gamete cells that are said to be **haploid**. The male haploid cells in flowering plants give rise to the pollen grains (sperm) whereas the female haploid cells give rise to eggs. As with animals, the diploid state is restored at fertilization by the union of DNA from the sperm and egg cells. Thus the plant life cycle is frequently divided into two major stages: the diploid stage (2N), which occurs after fertilization; and the haploid stage (1N), which occurs after meiosis.

A replicated chromosome consists of two identical sister chromatids that remain connected by a centromere. At mitosis, all the chromosomes attach their replicated and connected centromeres to a bipolar spindle apparatus. For each replicated chromosome, the two centromeres become attached to spindle fibers pointing in opposite directions (the metaphase stage of mitosis). Moving along the spindle fibers (the anaphase stage of mitosis), the sister chromatids of each replicated chromosome separate and move to opposite poles. Thus mitosis ensures that when a single cell divides into two, each new daughter cell is equipped with a complete and equal set of genetic instructions. After fertilization, the **zygote** grows into an embryo and then an adult by using mitosis until the time for sexual reproduction (flowering).

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

When producing sperm and egg cells for sexual reproduction, the genetic content must first be reduced from diploid to haploid. This reduction is accomplished by meiosis, a specialized process involving two sequential nuclear DNA divisions without an intervening DNA replication step. The first division requires the matching diploid chromosomes to pair, two-by-two, then segregate away from each other to reduce the genome from diploid to haploid. This chromosome pairing is necessary for proper chromosome segregation and much of the genetic shuffling that takes place from one generation to the next. The second meiotic division is like mitosis and divides replicated chromosomes into the haploid gamete-producing cells. Plant pollen mother cells that undergo meiosis provide excellent cytogenetic **specimens** to study because the cells and chromosomes are easy to see under the microscope.

specimen object or organism under consideration

Transposable Elements

Transposable DNA elements are sometimes called "jumping genes" because they can move around within the genome. The earliest evidence for the existence of these transposons came from analysis of certain strains of corn by McClintock. At the time in the 1940s, the idea that some parts of the chromosome could be mobile contradicted the notion that the chromosome was a stable, single structure. McClintock's pioneering work on transposons was formally recognized in 1983 when she was awarded a Nobel Prize. The activity of transposons sometimes causes visible features such as stripes and speckles on seeds (such as maize or beans) or flowers (such as petunias).

Transposons are active in most species of plants and animals, and their hopping around can change or even break individual genes. Thus transposons are thought to provide a source of genetic variation within the gene pool of a breeding population. In recent years, many plant transposons have been isolated molecularly (cloned) and used as tools to study plant genetics and create new genetic variations (mutations) by a technique called transposon mutagenesis. SEE ALSO Cell Cycle; Flowers; Genetic Engineering; McClintock, Barbara; Reproduction, Sexual.

Hank W. Bass

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Classification *See Taxonomy.*

Clements, Frederic

American Botanist
1874–1945

More than any scientist of his time, Frederic Clements (1874–1945) developed the methods and ideas that helped ecologists unravel nature's complexity. Indeed, ecology is arguably the most complex of all the sciences. The natural world that ecologists seek to understand is in constant flux. The weather and hundreds of other variables in the environment change from day to day, month to month, and from year to year. In any given habitat thousands of species and millions of individual plants and animals interact in a bewildering array of intricate associations.

When Clements arrived at the University of Nebraska in 1892 to begin studies in botany, the science of ecology was just beginning to crystallize from its diverse origins in plant **physiology**, plant geography, and plant **morphology**. Clements had been influenced by several European botanists, especially the German plant geographer Oscar Drude. Drawing on the ideas of Alexander von Humboldt, Drude had stressed the **holistic** nature of the plant community and the need for general theories of plant distribution rather than static descriptions of where different species lived. While studying at Nebraska, Clements began to formulate his own theory of plant associations. He soon became the leading ecologist in America during the early part of the twentieth century.

physiology the biochemical processes carried out by an organism

morphology shape and form

holistic including all the parts or factors that relate to an object or idea

Despite his stature, little has been written about Clements's life outside of his contributions to ecology and the plant sciences. We know that he received his doctoral degree from Nebraska in 1898 and married another Nebraska Ph.D. student, Edith Schwartz. The two collaborated on research and published numerous scientific books throughout their lives. After his studies at Nebraska, Clements joined the biology department at the University of Minnesota. In 1913, the Carnegie Institution of Washington helped Clements move his field studies to the Alpine Laboratory near Pikes Peak in Colorado. There Clements and his wife conducted detailed studies of environmental influences on plant associations, including the effects of temperature, humidity, light levels, and evaporation.

Early in his career, Clements set out to bring order to what was thought of as the chaotic and unsystematized state of ecology. Over a period of forty years, Clements developed a dynamic theory of plant communities that viewed plant associations as constantly changing rather than static, fixed entities. One of the major ideas that Clements used to understand ecological systems was the concept of vegetation as a super organism. To Clements, plant communities, like an animal's body, are comprised of interrelated parts, each vital to the functioning of the entire organism. Just like an individual organism, communities are born, grow, and mature, and then die.

Clements is best known for his theory of ecological succession. Building on the studies of Johannes Warming and Henry Chandler Cowles, Clements stated as a universal law that "all bare places give rise to new communities except those which present the most extreme conditions." Clements spent a lifetime studying vegetational changes in "bare places" such as ploughed fields or forests destroyed by fire. One of his major conclusions was that, in a given climatic area, all ecological successions lead to the same stable association of plant species. Clements called this final stage in a series of changes in plant communities the "climax state." While modern ecologists have rejected the theory of stable climax associations, Clements's pioneering ideas continue to influence our efforts to understand change and complexity in the natural world. SEE ALSO HUMBOLDT, ALEXANDER VON; WARMING, JOHANNES.

Bradford Carlton Lister

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Clines and Ecotypes

Clines and ecotypes are variants of a particular species adapted to a specific locale or set of environmental conditions. Charles Darwin (1809–1882) put forth his concept of evolution by natural selection to explain patterns of within species variation in 1859. Early-twentieth-century plant ecologists and **systematists** such as Frederic Clements (1874–1945) and Gote Turesson (1892–1970) recognized the usefulness of Darwin's theory and built on it. These plant biologists reasoned that variation within species reflects adaptations to specific environmental conditions.

systematists scientists who study systematics, the classification of species to reflect evolutionary relationships

population a group of organisms of a single species that exist in the same region and interbreed

herbivore an organism that feeds on plant parts

Different **populations** of the same species often grow across a range of environmental conditions, encompassing variation in moisture levels, soil composition, length of growing season, types and amounts of **herbivores**, and, for animal-pollinated species, even variation in the composition of the pollinators. These differences in environmental conditions may generate different selection pressures across the species range, resulting in genetic divergence among populations. For example, studies of Northern Hemisphere native plants often reveal that populations from more southern latitudes require shorter day length to flower than higher latitude populations of the same species. Natural selection has favored individuals found at higher latitudes to flower later, when conditions are more favorable for growth and when pollinators are abundant. In many examples researchers have conducted transplant experiments, taking plants from one locale and growing them in the site of another population of the same species. Often the transplants perform less successfully than plants from the home locale, demonstrating that the two populations are genetically diverged in terms of their adaptation to local environmental conditions (see Briggs and Walters, 1984, for examples).

Sand verbena and dune evening primrose bloom at night, adapted to the desert conditions of Joshua Tree National Monument in California.

These genetically based adaptations to the environment were first termed "ecotypes" by Turesson. The ecotype concept integrates the type concept of systematists, who group organisms that are most similar to the type specimen (the "ideal" representative of the species) with the realization that within-species variation has important ecological significance. The ecotype concept suggests that variation is discrete or discontinuous and early critics noted that important environmental variation, such as the day length example, is continuous and graded. Thus to the ecotype concept was added the notion of clinal variation, such that continuous variation of traits would reflect responses by populations to environmental selective agents. The demonstration of ecotypes and clines was very important to the confirmation of Darwin's theory of evolution by natural selection and continues to provide insight into the mechanisms of evolution of biological variation.

The recognition of ecotypic and clinal variation has also figured prominently in the development of conservation and restoration policy of biodiversity. The primary concerns are the permanent loss of adaptive genetic variation as rare plants become reduced to few populations, deciding which populations to save based on strategies to maximize the species range, and the adaptation of captive populations (in zoos or botanical gardens) to their captive environment at the cost of their ability to survive in their native wild environment. Most of the current questions in the study of biodiversity revolve around our limited understanding of the genetics of adaptations, in particular how rapidly populations can evolve ecotypes. This, in turn, depends on the amount of genetic variation maintained within populations and the ability of new mutations to contribute to adaptive change. SEE ALSO BIOGEOGRAPHY; BIOME; CLEMENTS, FREDERIC; DARWIN, CHARLES.

Charles B. Fenster and Hans K. Stenøien

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Glossary

abiotic nonliving

abrade to wear away through contact

abrasive tending to wear away through contact

abscission dropping off or separating

accession a plant that has been acquired and catalogued

achene a small, dry, thin-walled type of fruit

actinomycetes common name for a group of Gram-positive bacteria that are filamentous and superficially similar to fungi

addictive capable of causing addiction or chemical dependence

adhesion sticking to the surface of

adventitious arising from secondary buds, or arising in an unusual position

aeration the introduction of air

albuminous gelatinous, or composed of the protein albumin

alkali chemically basic; the opposite of acidic

alkalinization increase in basicity or reduction in acidity

alkaloid bitter secondary plant compound, often used for defense

allele one form of a gene

allelopathy harmful action by one plant against another

allopolyploidy a polyploid organism formed by hybridization between two different species or varieties (*allo* = other)

alluvial plain broad area formed by the deposit of river sediment at its outlet

amended soils soils to which fertilizers or other growth aids have been added

amendment additive

anaerobic without oxygen

analgesic pain-relieving

analog a structure or thing, especially a chemical, similar to something else

angiosperm a flowering plant

anomalous unusual or out of place

anoxic without oxygen

antenna system a collection of protein complexes that harvests light energy and converts it to excitation energy that can migrate to a reaction center; the light is absorbed by pigment molecules (e.g., chlorophyll, carotenoids, phycobilin) that are attached to the protein

anthropogenic human-made; related to or produced by the influence of humans on nature

antibodies proteins produced to fight infection

antioxidant a substance that prevents damage from oxygen or other reactive substances

apical meristem region of dividing cells at the tips of growing plants

apical at the tip

apomixis asexual reproduction that may mimic sexual reproduction

appendages parts that are attached to a central stalk or axis

arable able to be cultivated for crops

Arcto-Tertiary geoflora the fossil flora discovered in Arctic areas dating back to the Tertiary period; this group contains magnolias (*Magnolia*), tulip trees (*Liriodendron*), maples (*Acer*), beech (*Fagus*), black gum (*Nyssa*), sweet gum (*Liquidambar*), dawn redwood (*Metasequoia*), cypress (*Taxodium*), and many other species

artifacts pots, tools, or other cultural objects

assayer one who performs chemical tests to determine the composition of a substance

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

attractant something that attracts

autotroph "self-feeder"; any organism that uses sunlight or chemical energy

auxin a plant hormone

avian related to birds

axil the angle or crotch where a leaf stalk meets the stem

axillary bud the bud that forms in the angle between the stem and leaf

basipetal toward the base

belladonna the source of atropine; means "beautiful woman," and is so named because dilated pupils were thought to enhance a woman's beauty

binomial two-part

biodirected assays tests that examine some biological property

biodiversity degree of variety of life

biogeography the study of the reasons for the geographic distribution of organisms

biomass the total dry weight of an organism or group of organisms

biosphere the region of the Earth in which life exists

biosynthesis creation through biological pathways

biota the sum total of living organisms in a region of a given size

biotic involving or related to life

bryologist someone who studies bryophytes, a division of nonflowering plants

campanulate bell-shaped

capitulum the head of a compound flower, such as a dandelion

cardiotonic changing the contraction properties of the heart

carotenoid a yellow-colored molecule made by plants

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

catastrophism the geologic doctrine that sudden, violent changes mark the geologic history of Earth

cation positively charged particle

catkin a flowering structure used for wind pollination

centrifugation spinning at high speed in a centrifuge to separate components

chitin a cellulose-like molecule found in the cell wall of many fungi and arthropods

chloroplast the photosynthetic organelle of plants and algae

circadian “about a day”; related to a day

circumscription the definition of the boundaries surrounding an object or an idea

cisterna a fluid-containing sac or space

clade a group of organisms composed of an ancestor and all of its descendants

cladode a modified stem having the appearance and function of a leaf

coalescing roots roots that grow together

coleoptile the growing tip of a monocot seedling

collenchyma one of three cell types in ground tissue

colonize to inhabit a new area

colony a group of organisms inhabiting a particular area, especially organisms descended from a common ancestor

commensalism a symbiotic association in which one organism benefits while the other is unaffected

commodities goods that are traded, especially agricultural goods

community a group of organisms of different species living in a region

compaction compacting of soil, leading to the loss of air spaces

complex hybrid hybridized plant having more than two parent plants

compound a substance formed from two or more elements

concentration gradient a difference in concentration between two areas

continental drift the movement of continental land masses due to plate tectonics

contractile capable of contracting

convective uplift the movement of air upwards due to heating from the sun

coppice growth the growth of many stems from a single trunk or root, following the removal of the main stem

cortical relating to the cortex of a plant

covalent held together by electron-sharing bonds

crassulacean acid metabolism water-conserving strategy used by several types of plants

crop rotation alternating crops from year to year in a particular field

cultivation growth of plants, or turning the soil for growth of crop plants

crystallography the use of x-rays on crystals to determine molecular structure

cuticle the waxy outer coating of a leaf or other structure, which provides protection against predators, infection, and water loss

cyanide heap leach gold mining a technique used to extract gold by treating ore with cyanide

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

cyanogenic giving rise to cyanide

cytologist a scientist who studies cells

cytology the microscopic study of cells and cell structure

cytosol the fluid portion of a cell

cytostatic inhibiting cell division

deductive reasoning from facts to conclusion

dendrochronologist a scientist who uses tree rings to determine climate or other features of the past

dermatophytes fungi that cause skin diseases

desertification degradation of dry lands, reducing productivity

desiccation drying out

detritus material from decaying organisms

diatoms hard-shelled, single-celled marine organisms; a type of algae

dictyosome any one of the membranous or vesicular structures making up the Golgi apparatus

dioicous having male and female sexual parts on different plants

diploid having two sets of chromosomes, versus having one set (haploid)

dissipate to reduce by spreading out or scattering

distal further away from

diurnal daily, or by day

domestication the taming of an organism to live with and be of use to humans

dormant inactive, not growing

drupe a fruit with a leathery or stone-like seed

dynamical system theory the mathematical theory of change within a system

ecophysiological related to how an organism's physiology affects its function in an ecosystem

ecosystem an ecological community and its environment

elater an elongated, thickened filament

empirical formula the simplest whole number ratio of atoms in a compound

emulsifier a chemical used to suspend oils in water

encroachment moving in on

endemic belonging or native to a particular area or country

endophyte a fungus that lives within a plant

endoplasmic reticulum the membrane network inside a cell

endosperm the nutritive tissue in a seed, formed by the fertilization of a diploid egg tissue by a sperm from pollen

endosporic the formation of a gametophyte inside the spore wall

endosymbiosis a symbiosis in which one organism lives inside the other

Enlightenment eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

entomologist a scientist who studies insects

enzyme a protein that controls a reaction in a cell

ephemeral short-lived

epicuticle the waxy outer covering of a plant, produced by the epidermis

epidermis outer layer of cells

epiphytes plants that grow on other plants

escarpment a steep slope or cliff resulting from erosion

ethnobotanist a scientist who interacts with native peoples to learn more about the plants of a region

ethnobotany the study of traditional uses of plants within a culture

euglossine bees a group of bees that pollinate orchids and other rainforest plants

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

extrafloral outside the flower

exudation the release of a liquid substance; oozing

facultative capable of but not obligated to

fertigation application of small amounts of fertilizer while irrigating

filament a threadlike extension

filamentous thin and long

flagella threadlike extension of the cell membrane, used for movement

flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

florigen a substance that promotes flowering

floristic related to plants

follicle sac or pouch

forbs broad-leaved, herbaceous plants

free radicals toxic molecular fragments

frugivous feeding on fruits

gametangia structure where gametes are formed

gametophyte the haploid organism in the life cycle

gel electrophoresis a technique for separating molecules based on size and electrical charge

genera plural of genus; a taxonomic level above species

genome the genetic material of an organism

genotype the genetic makeup of an organism

germplasm hereditary material, especially stored seed or other embryonic forms

globose rounded and swollen; globe-shaped

gradient difference in concentration between two places

green manure crop planted to be plowed under to nourish the soil, especially with nitrogen

gymnosperm a major group of plants that includes the conifers

gynoecium the female reproductive organs as a whole

gypsipherous containing the mineral gypsum

hallucinogenic capable of inducing hallucinations

haploid having one set of chromosomes, versus having two (diploid)

haustorial related to a haustorium, or food-absorbing organ

hemiterpene a half terpene

herbivore an organism that feeds on plant parts

heterocyclic a chemical ring structure composed of more than one type of atom, for instance carbon and nitrogen

heterosporous bearing spores of two types, large megaspores and small microspores

heterostylous having styles (female flower parts) of different lengths, to aid cross-pollination

heterotroph an organism that derives its energy from consuming other organisms or their body parts

holistic including all the parts or factors that relate to an object or idea

homeotic relating to or being a gene that produces a shift in structural development

homology a similarity in structure between anatomical parts due to descent from a common ancestor

humus the organic material in soil formed from decaying organisms

hybrid a mix of two varieties or species

hybridization formation of a new individual from parents of different species or varieties

hydrological cycle the movement of water through the biosphere

hydrophobic water repellent

hydroponic growing without soil, in a watery medium

hydroxyl the chemical group -OH

hyphae the threadlike body mass of a fungus

illicit illegal

impede to slow down or inhibit

inert incapable of reaction

inflorescence a group of flowers or arrangement of flowers in a flower head

infrastructure roads, phone lines, and other utilities that allow commerce

insectivorous insect-eating

intercalary inserted; between

interspecific hybridization hybridization between two species

intertidal between the lines of high and low tide

intracellular bacteria bacteria that live inside other cells

intraspecific taxa levels of classification below the species level

intuiting using intuition

ionic present as a charged particle

ions charged particles

irreversible unable to be reversed

juxtaposition contrast brought on by close positioning

lacerate cut

Lamarckian inheritance the hypothesis that acquired characteristics can be inherited

lamellae thin layers or plate-like structure

land-grant university a state university given land by the federal government on the condition that it offer courses in agriculture

landrace a variety of a cultivated plant, occurring in a particular region

lateral to the side of

legume beans and other members of the Fabaceae family

lignified composed of lignin, a tough and resistant plant compound

lineage ancestry; the line of evolutionary descent of an organism

loci (singular: locus) sites or locations

lodging falling over while still growing

lytic breaking apart by the action of enzymes

macromolecule a large molecule such as a protein, fat, nucleic acid, or carbohydrate

macroscopic large, visible

medulla middle part

megaphylls large leaves having many veins or a highly branched vein system

meiosis the division of chromosomes in which the resulting cells have half the original number of chromosomes

meristem the growing tip of a plant

mesic of medium wetness

microfibrils microscopic fibers in a cell

micron one millionth of a meter; also called micrometer

microphylls small leaves having a single unbranched vein

mitigation reduction of amount or effect

mitochondria cell organelles that produce adenosine triphosphate (ATP) to power cell reactions

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

molecular systematics the analysis of DNA and other molecules to determine evolutionary relationships

monoculture a large stand of a single crop species

monomer a single unit of a multi-unit structure

monophyletic a group that includes an ancestral species and all its descendants

montane growing in a mountainous region

morphology shape and form

motile capable of movement

mucilaginous sticky or gummy

murein a peptidoglycan, a molecule made up of sugar derivatives and amino acids

mutualism a symbiosis between two organisms in which both benefit

mycelium the vegetative body of a fungus, made up of threadlike hyphae

$NADP^+$ oxidized form of nicotinamide adenine dinucleotide phosphate

NADPH reduced form of nicotinamide adenine dinucleotide phosphate, a small, water-soluble molecule that acts as a hydrogen carrier in biochemical reactions

nanometer one billionth of a meter

nectaries organs in flowers that secrete nectar

negative feedback a process by which an increase in some variable causes a response that leads to a decrease in that variable

neuromuscular junction the place on the muscle surface where the muscle receives stimulus from the nervous system

neurotransmitter a chemical that passes messages between nerve cells

node branching site on a stem

nomenclature a naming system

nonmotile not moving

nonpolar not directed along the root-shoot axis, or not marked by separation of charge (unlike water and other polar substances)

nonsecretory not involved in secretion, or the release of materials

Northern Blot a technique for separating RNA molecules by electrophoresis and then identifying a target fragment with a DNA probe

nucleolar related to the nucleolus, a distinct region in the nucleus

nurseryman a worker in a plant nursery

obligate required, without another option

obligate parasite a parasite without a free-living stage in the life cycle

odorant a molecule with an odor

organelle a membrane-bound structure within a cell

osmosis the movement of water across a membrane to a region of high solute concentration

oviposition egg-laying

oxidation reaction with oxygen, or loss of electrons in a chemical reaction

paleobotany the study of ancient plants and plant communities

pangenesis the belief that acquired traits can be inherited by bodily influences on the reproductive cells

panicle a type of inflorescence (flower cluster) that is loosely packed and irregularly branched

paraphyletic group a taxonomic group that excludes one or more descendants of a common ancestor

parenchyma one of three types of cells found in ground tissue

pastoralists farming people who keep animal flocks

pathogen disease-causing organism

pedicel a plant stalk that supports a fruiting or spore-bearing organ

pentamerous composed of five parts

percolate to move through, as a fluid through a solid

peribacteroid a membrane surrounding individual or groups of rhizobia bacteria within the root cells of their host; in such situations the bacteria

have frequently undergone some change in surface chemistry and are referred to as bacteroids

pericycle cell layer between the conducting tissue and the endodermis

permeability the property of being permeable, or open to the passage of other substances

petiole the stalk of a leaf, by which it attaches to the stem

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral. Low pH numbers indicate high acidity while high numbers indicate alkalinity

pharmacognosy the study of drugs derived from natural products

pharmacopeia a group of medicines

phenology seasonal or other time-related aspects of an organism's life

pheromone a chemical released by one organism to influence the behavior of another

photooxidize to react with oxygen under the influence of sunlight

photoperiod the period in which an organism is exposed to light or is sensitive to light exposure, causing flowering or other light-sensitive changes

photoprotectant molecules that protect against damage by sunlight

phylogenetic related to phylogeny, the evolutionary development of a species

physiology the biochemical processes carried out by an organism

phytogeographer a scientist who studies the distribution of plants

pigments colored molecules

pistil the female reproductive organ of a flower

plasmodesmata cell-cell junctions that allow passage of small molecules between cells

polyculture mixed species

polyhedral in the form of a polyhedron, a solid whose sides are polygons

polymer a large molecule made from many similar parts

polynomial "many-named"; a name composed of several individual parts

polyploidy having multiple sets of chromosomes

polysaccharide a linked chain of many sugar molecules

population a group of organisms of a single species that exist in the same region and interbreed

porosity openness

positive feedback a process by which an increase in some variable causes a response that leads to a further increase in that variable

precipitation rainfall; or the process of a substance separating from a solution

pre-Columbian before Columbus

precursor a substance from which another is made

predation the act of preying upon; consuming for food

primordial primitive or early

progenitor parent or ancestor

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

propagate to create more of through sexual or asexual reproduction

protist a usually single-celled organism with a cell nucleus, of the kingdom Protista

protoplasmic related to the protoplasm, cell material within the cell wall

protoplast the portion of a cell within the cell wall

psychoactive causing an effect on the brain

pubescence covered with short hairs

pyruvic acid a three-carbon compound that forms an important intermediate in many cellular processes

quadruple hybrid hybridized plant with four parents

quantitative numerical, especially as derived from measurement

quid a wad for chewing

quinone chemical compound found in plants, often used in making dyes

radii distance across, especially across a circle (singular = radius)

radioisotopes radioactive forms of an element

rambling habit growing without obvious intended direction

reaction center a protein complex that uses light energy to create a stable charge separation by transferring a single electron energetically uphill from a donor molecule to an acceptor molecule, both of which are located in the reaction center

redox oxidation and reduction

regurgitant material brought up from the stomach

Renaissance a period of artistic and intellectual expansion in Europe from the fourteenth to the sixteenth century

salinization increase in salt content

samara a winged seed

saprophytes plants that feed on decaying parts of other plants

saturated containing as much dissolved substance as possible

sclerenchyma one of three cell types in ground tissue

sedimentation deposit of mud, sand, shell, or other material

semidwarf a variety that is intermediate in size between dwarf and full-size varieties

senescent aging or dying

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

sequester to remove from circulation; lock up

serology the study of serum, the liquid, noncellular portion of blood

seta a stiff hair or bristle

silage livestock food produced by fermentation in a silo

siliceous composed of silica, a mineral

silicified composed of silicate minerals

soil horizon distinct layers of soil

solute a substance dissolved in a solution

Southern blot a technique for separating DNA fragments by electrophoresis and then identifying a target fragment with a DNA probe

spasticity abnormal muscle activity caused by damage to the nerve pathways controlling movement

speciation the creation of new species

specimen an object or organism under consideration

speciose marked by many species

sporophyte the diploid, spore-producing individual in the plant life cycle

sporulate to produce or release spores

sterile not capable or involved in reproduction, or unable to support life

sterols chemicals related to steroid hormones

stolons underground stems that may sprout and form new individuals

stomata openings between guard cells on the underside of leaves that allow gas exchange

stratification layering, or separation in space

stratigraphic geology the study of rock layers

stratigraphy the analysis of strata (layered rock)

strobili cone-like reproductive structures

subalpine a region less cold or elevated than alpine (mountaintop)

substrate the physical structure to which an organism attaches, or a molecule acted on by enzymes

succession the pattern of changes in plant species that occurs after a soil disturbance

succulent fleshy, moist

suckers naturally occuring adventitious shoots

suffrutescent a shrub-like plant with a woody base

sulfate a negatively charged particle combining sulfur and oxygen

surfaced smoothed for examination

susceptibility vulnerability

suture line of attachment

swidden agriculture the practice of farming an area until the soil has been depleted and then moving on

symbiont one member of a symbiotic association

symbiosis a relationship between organisms of two different species in which at least one benefits

systematists scientists who study systematics, the classification of species to reflect evolutionary relationships

systemic spread throughout the plant

tannins compounds produced by plants that usually serve protective functions, often colored and used for “tanning” and dyeing

taxa a type of organism, or a level of classification of organisms

tensile forces forces causing tension, or pulling apart; the opposite of compression

tepal an undifferentiated sepal or petal

Tertiary period geologic period from sixty-five to five million years ago

tetraploid having four sets of chromosomes; a form of polyploidy

thallus simple, flattened, nonleafy plant body

tilth soil structure characterized by open air spaces and high water storage capacity due to high levels of organic matter

tonoplast the membrane of the vacuole

topographic related to the shape or contours of the land

totipotent capable of forming entire plants from individual cells

toxin a poisonous substance

tracheid a type of xylem cell that conducts water from root to shoot

transcription factors proteins that bind to a specific DNA sequence called the promoter to regulate the expression of a nearby gene

translocate to move materials from one region to another

translucent allowing the passage of light

transmutation to change from one form to another

transpiration movement of water from soil to atmosphere through a plant

transverse across, or side to side

tribe a group of closely related genera

trophic related to feeding

turgor pressure the outward pressure exerted on the cell wall by the fluid within

twining twisting around while climbing

ultrastructural the level of structure visible with the electron microscope; very small details of structure

uniformitarian the geologic doctrine that formative processes on earth have proceeded at the same rate through time since earth's beginning

uplift raising up of rock layers, a geologic process caused by plate tectonics

urbanization increase in size or number of cities

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Used for storage and maintaining internal pressure

vascular plants plants with specialized transport cells; plants other than bryophytes

vascular related to the transport of nutrients, or related to blood vessels

vector a carrier, usually one that is not affected by the thing carried

vernal related to the spring season

vesicle a membrane-bound cell structure with specialized contents

viable able to live or to function

volatile easily released as a gas

volatilization the release of a gaseous substance

water table the level of water in the soil

whorl a ring

wort an old English term for plant; also an intermediate liquid in beer making

xenobiotics biomolecules from outside the plant, especially molecules that are potentially harmful

xeromorphic a form adapted for dry conditions

xerophytes plants adapted for growth in dry areas

zonation division into zones having different properties

zoospore a swimming spore

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

Topic Outline

ADAPTATIONS

Alkaloids
Allelopathy
Cacti
Cells, Specialized Types
Clines and Ecotypes
Defenses, Chemical
Defenses, Physical
Halophytes
Lichens
Mycorrhizae
Nitrogen Fixation
Poisonous Plants
Seed Dispersal
Shape and Form of Plants
Symbiosis
Translocation
Trichomes

AGRICULTURE

Agriculture, History of
Agriculture, Modern
Agriculture, Organic
Agricultural Ecosystems
Agronomist
Alliaceae
Asteraceae
Biofuels
Borlaug, Norman
Breeder
Breeding
Burbank, Luther
Cacao
Carver, George W.
Coffee
Compost
Cork
Corn
Cotton
Economic Importance of Plants
Ethnobotany
Fertilizer
Fiber and Fiber Products
Food Scientist
Fruits
Fruits, Seedless
Genetic Engineer
Genetic Engineering
Grains
Grasslands
Green Revolution
Halophytes
Herbs and Spices
Herbicides
Horticulture
Horticulturist
Hydroponics
Native Food Crops
Nitrogen Fixation
Oils, Plant-Derived
Pathogens
Pathologist
Polyploidy
Potato
Potato Blight
Quantitative Trait Loci
Rice
Seed Preservation
Soil, Chemistry of
Soil, Physical Characteristics
Solanaceae
Soybeans
Sugar
Tea
Tissue Culture

Tobacco
Transgenic Plants
Vavilov, N. I.
Vegetables
Weeds
Wheat
Wine and Beer Industry

ANATOMY

Anatomy of Plants
Bark
Botanical and Scientific Illustrator
Cell Walls
Cells
Cells, Specialized Types
Cork
Differentiation and Development
Fiber and Fiber Products
Flowers
Fruits
Inflorescence
Leaves
Meristems
Mycorrhizae
Phyllotaxis
Plants
Roots
Seeds
Shape and Form of Plants
Stems
Tissues
Tree Architecture
Trichomes
Vascular Tissues
Vegetables
Wood Anatomy

BIOCHEMISTRY/PHYSIOLOGY

Alcoholic Beverage Industry
Alkaloids
Anthocyanins
Biofuels
Biogeochemical Cycles
Bioremediation
Carbohydrates
Carbon Cycle
Cells
Cellulose
Chlorophyll
Chloroplasts
Cytokinins
Defenses, Chemical
Ecology, Energy Flow
Fertilizer
Flavonoids
Flavor and Fragrance Chemist
Halophytes
Herbicides
Hormones
Lipids
Medicinal Plants
Nitrogen Fixation
Nutrients
Oils, Plant-Derived
Pharmaceutical Scientist
Photoperiodism
Photosynthesis, Carbon Fixation
Photosynthesis, Light Reactions
Physiologist
Pigments
Poisonous Plants
Psychoactive Plants
Soil, Chemistry of
Terpenes
Translocation
Vacuoles
Water Movement

BIODIVERSITY

Agricultural Ecosystems
Aquatic Ecosystems
Biodiversity
Biogeography
Biome
Botanical Gardens and Arboreta
Chapparal
Clines and Ecotypes
Coastal Ecosystems
Coniferous Forests
Curator of a Botanical Garden
Curator of an Herbarium
Deciduous Forests
Deforestation
Desertification
Deserts
Ecology
Ethnobotany
Global Warning
Herbaria
Human Impacts
Invasive Species

Plant Prospecting
Rain Forest Canopy
Rain Forests
Savanna
Taxonomist
Tundra
Wetlands

BIOMES

Aquatic Ecosystems
Atmosphere and Plants
Biodiversity
Biogeography
Biome
Cacti
Chapparal
Coastal Ecosystems
Coniferous Forests
Deciduous Forests
Deforestation
Desertification
Deserts
Ecology
Ecosystem
Global Warning
Grasslands
Human Impacts
Invasive Species
Peat Bogs
Plant Prospecting
Rain Forest Canopy
Rain Forests
Savanna
Tundra
Wetlands

CAREERS

Agriculture, Modern
Agriculture, Organic
Agronomist
Alcoholic Beverage Industry
Arborist
Botanical and Scientific Illustrator
Breeder
Breeding
College Professor
Curator of a Botanical Garden
Curator of an Herbarium
Flavor and Fragrance Chemist
Food Scientist
Forester
Forestry
Genetic Engineer
Genetic Engineering
Horticulture
Horticulturist
Landscape Architect
Pathologist
Pharmaceutical Scientist
Physiologist
Plant Prospecting
Taxonomist
Turf Management

CELL BIOLOGY

Algae
Biogeochemical Cycles
Cell Cycle
Cell Walls
Cells
Cells, Specialized Types
Cellulose
Chloroplasts
Cork
Differentiation and Development
Embryogenesis
Fiber and Fiber Products
Germination
Germination and Growth
Leaves
Meristems
Molecular Plant Genetics
Mycorrhizae
Nitrogen Fixation
Physiologist
Plastids
Reproduction, Fertilization
Roots
Seeds
Stems
Tissues
Translocation
Trichomes
Tropisms and Nastic Movements
Vacuoles
Vascular Tissues
Water Movement
Wood Anatomy

DESERTS

Biome
Cacti

Desertification
Deserts
Ecosystem
Halophytes
Native Food Crops
Photosynthesis, Carbon Fixation and
Tundra

DISEASES OF PLANTS

Acid Rain
Chestnut Blight
Deforestation
Dutch Elm Disease
Fungi
Interactions, Plant-Fungal
Interactions, Plant-Insect
Nutrients
Pathogens
Pathologist
Potato Blight

DRUGS AND POISONS

Alcoholic Beverage Industry
Alcoholic Beverages
Alkaloids
Cacao
Cannabis
Coca
Coffee
Defenses, Chemical
Dioscorea
Economic Importance of Plants
Ethnobotany
Flavonoids
Medicinal Plants
Pharmaceutical Scientist
Plant Prospecting
Poison Ivy
Poisonous Plants
Psychoactive Plants
Solanaceae
Tea
Tobacco

ECOLOGY

Acid Rain
Agricultural Ecosystems
Aquatic Ecosystems
Atmosphere and Plants
Biodiversity
Biogeochemical Cycles
Biogeography
Biome
Carbon Cycle
Chapparal
Clines and Ecotypes
Coastal Ecosystems
Coniferous Forests
Deciduous Forests
Decomposers
Defenses, Chemical
Defenses, Physical
Deforestation
Desertification
Deserts
Ecology
Ecology, Energy Flow
Ecology, Fire
Ecosystem
Endangered Species
Global Warning
Grasslands
Human Impacts
Interactions, Plant-Fungal
Interactions, Plant-Insect
Interactions, Plant-Plant
Interactions, Plant-Vertebrate
Invasive Species
Mycorrhizae
Nutrients
Pathogens
Peat Bogs
Pollination Biology
Rain Forest Canopy
Rain Forests
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Shape and Form of Plants
Soil, Chemistry of
Soil, Physical Characteristics
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ECONOMIC IMPORTANCE OF PLANTS

Acid Rain
Agricultural Ecosystems
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Agriculture, Modern
Agriculture, Organic

Alcoholic Beverage Industry
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Bamboo
Biofuels
Bioremediation
Breeder
Cacao
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Chestnut Blight
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Coniferous Forests
Cork
Corn
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Economic Importance of Plants
Fiber and Fiber Products
Flavor and Fragrance Chemist
Fruits
Fruits, Seedless
Food Scientist
Forensic Botany
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Genetic Engineer
Global Warning
Grains
Green Revolution
Herbs and Spices
Horticulture
Horticulturist
Human Impacts
Hydroponics
Landscape Architect
Medicinal Plants
Oils, Plant-Derived
Ornamental Plants
Paper
Peat Bogs
Pharmaceutical Scientist
Plant Prospecting
Potato Blight
Rice
Soybeans
Sugar
Tea
Turf Management
Wheat
Wood Products
Vegetables

EVOLUTION

Algae
Angiosperms
Archaea
Biodiversity
Biogeography
Breeding Systems
Bryophytes
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plant sciences

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Preface

Someone once said that if you want to find an alien life form, just go into your backyard and grab the first green thing you see. Although plants evolved on Earth along with the rest of us, they really are about as different and strange and wonderful a group of creatures as one is likely to find anywhere in the universe.

The World of Plants

Consider for a minute just how different plants are. They have no mouths, no eyes or ears, no brain, no muscles. They stand still for their entire lives, planted in the soil like enormous drinking straws wicking gallon after gallon of water from the earth to the atmosphere. Plants live on little more than water, air, and sunshine and have mastered the trick of transmuting these simple things into almost everything they (and we) need. In this encyclopedia, readers will find out how plants accomplish this photosynthetic alchemy and learn about the extraordinary variety of form and function within the plant kingdom. In addition, readers will be able to trace their 450-million-year history and diversification, from the very first primitive land plants to the more than 250,000 species living today.

✶Explore further in Photosynthesis, Light Reactions and Evolution of Plants

All animals ultimately depend on photosynthesis for their food, and humans are no exception. Over the past ten thousand years, we have cultivated such an intimate relationship with a few species of grains that it is hardly an exaggeration to say, in the words of one scientist, that "humans domesticated wheat, and vice versa." With the help of agriculture, humans were transformed from a nomadic, hunting and gathering species numbering in the low millions, into the most dominant species on the planet, with a population that currently exceeds six billion. Agriculture has shaped human culture profoundly, and together the two have reshaped the planet. In this encyclopedia, readers can explore the history of agriculture, learn how it is practiced today, both conventionally and organically, and what the impact of it and other human activities has been on the land, the atmosphere, and the other creatures who share the planet with us.

✶Explore further in Agriculture, Modern and Human Impacts

Throughout history—even before the development of the modern scientific method—humans experimented with plants, finding the ones that provided the best meal, the strongest fiber, or the sweetest wine. Naming a thing is such a basic and powerful way of knowing it that all cultures have created some type of taxonomy for the plants they use. The scientific understanding of plants through experimentation, and the development of ra-

tional classification schemes based on evolution, has a rich history that is explored in detail in this encyclopedia. There are biographies of more than two dozen botanists who shaped our modern understanding, and essays on the history of physiology, ecology, taxonomy, and evolution. Across the spectrum of the botanical sciences, progress has accelerated in the last two decades, and a range of entries describe the still-changing understanding of evolutionary relationships, genetic control, and biodiversity.

✶Explore further in Ecology, History of; Biodiversity; and Phylogeny

With the development of our modern scientific society, a wide range of new careers has opened up for people interested in plant sciences, many of which are described in this encyclopedia. Most of these jobs require a college degree, and the better-paying ones often require advanced training. While all are centered around plants, they draw on skills that range from envisioning a landscape in one's imagination (landscape architect) to solving differential equations (an ecological modeler) to budgeting and personnel management (curator of a botanical garden).

✶Explore further in Curator of a Botanical Garden and Landscape Architect

Organization of the Material

Each of the 280 entries in *Plant Sciences* has been newly commissioned for this work. Our contributors are drawn from academic and research institutions, industry, and nonprofit organizations throughout North America. In many cases, the authors literally "wrote the book" on their subject, and all have brought their expertise to bear in writing authoritative, up-to-date entries that are nonetheless accessible to high school students. Almost every entry is illustrated and there are numerous photos, tables, boxes, and sidebars to enhance understanding. Unfamiliar terms are highlighted and defined in the margin. Most entries are followed by a list of related articles and a short reading list for readers seeking more information. Front and back matter include a geologic timescale, a topic outline that groups entries thematically, and a glossary. Each volume has its own index, and volume 4 contains a cumulative index covering the entire encyclopedia.

Acknowledgments and Thanks

I wish to thank the many people at Macmillan Reference USA and the Gale Group for their leadership in bringing this work to fruition, and their assiduous attention to the many details that make such a work possible. In particular, thanks to Hélène Potter, Brian Kinsey, Betz Des Chenes, and Diane Sawinski. The editorial board members—Robert Evans, Wendy Mechaber, and Robert Wallace—were outstanding, providing invaluable expertise and extraordinary hard work. Wendy is also my wife, and I wish to thank her for her support and encouragement throughout this project. My own love of plants began with three outstanding biology teachers, Marjorie Holland, James Howell, and Walt Tulecke, and I am in their debt. My many students at the Commonwealth School in Boston were also great teachers—their enthusiastic questions over the years deepened my own understanding and appreciation of the mysteries of the plant world. I hope that a new generation of students can discover some of the excitement and mystery of this world in *Plant Sciences*.

Richard Robinson
Editor in Chief

Geologic Timescale

Era	Period		Epoch	started (millions of years ago)
Cenozoic 66.4 millions of years ago–present time	**Quaternary**		Holocene	0.01
			Pleistocene	1.6
	Tertiary	**Neogene**	Pliocene	5.3
			Miocene	23.7
		Paleogene	Oligocene	36.6
			Eocene	57.8
			Paleocene	66.4
Mesozoic 245–66.4 millions of years ago	**Cretaceous**		Late	97.5
			Early	144
	Jurassic		Late	163
			Middle	187
			Early	208
	Triassic		Late	230
			Middle	240
			Early	245
Paleozoic 570–245 millions of years ago	**Permian**		Late	258
			Early	286
	Carboniferous	**Pennsylvanian**	Late	320
		Mississippian	Early	360
	Devonian		Late	374
			Middle	387
			Early	408
	Silurian		Late	421
			Early	438
	Ordovician		Late	458
			Middle	478
			Early	505
	Cambrian		Late	523
			Middle	540
			Early	570
Precambrian time 4500–570 millions of years ago				4500

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Coastal Ecosystems

An ecosystem is an interacting **community** of organisms and their nonliving physical environment occupying a certain place and time. Coastal ecosystems occupy the margins of the land and the sea. There are many different types: salt marshes, mangrove swamps, sand dunes, seagrass meadows, coral reefs, kelp forests, tidal flats, rocky **intertidal**, maritime forests, and coastal heathlands. All are heavily influenced by some combination of saltwater, ocean waves, currents, and ocean breezes, though not necessarily all of these.

community a group of organisms of different species living in a region

intertidal between the lines of high and low tide

Components of Coastal Ecosystems

The major interactions of organisms and their environment in coastal ecosystems include energy transfer and cycling of materials. These involve several functional groups of organisms. Plants and algae are the major primary producers, that is, organisms that produce their own food through the process of photosynthesis. They use the energy from the sun and the nutrients washed down to the coast from the surrounding land or brought to the coast by the ocean.

The plants living in constant or periodic contact with ocean water are called halophytes ("salt plants"). They must have special adaptations to be able to thrive because saltwater is toxic to most plants.

Plants and algae are the bases of the coastal food chain. They may be consumed by **herbivores**, such as insects or geese that feed on salt marsh grasses, snails that consume seaweeds on rocky shores, or fish that graze on tropical seagrass beds. Except for the intertidal marshes and mangrove swamps, the place of insects in coastal ecosystems is minor, their ecological role being replaced by crustaceans (such as crabs, shrimp, lobsters, and beach fleas) and mollusks (snails, clams, mussels, etc.) All these, in turn, may become food for carnivores, such as birds (shorebirds, waterfowl, hawks, etc.) or fish. Many animals living in coastal ecosystems do not feed directly on plants or other animals but feed on **detritus**, nonliving plant material that may contain a large amount of bacteria and fungi. The bacteria and fungi that **colonize** particles of detritus act to break down this material to simple chemical compounds that can be recycled.

herbivore an organism that feeds on plant parts

detritus material from decaying organisms

The rich underwater ecosystem of a mangrove swamp on Palawan Island in the Philippines.

Coastal versus Terrestrial Ecosystems

Coastal ecosystems differ from terrestrial ones in several significant ways. The ocean contributes to the exchange of materials, bringing nutrients and removing waste products. In terrestrial ecosystems, the exchange of materials between organisms and their environment does not involve this major mediating agent.

The dominant types of producer organisms in terrestrial ecosystems are plants. In coastal ecosystems they include plants, macroalgae (seaweeds), and phytoplankton (unicellular algae). Seaweeds reach their greatest level of diversity and productivity in coastal ecosystems.

Estuaries

An estuary is a semienclosed body of water where freshwater meets the sea. Typically located at the mouth of rivers, estuaries have characteristics of both fresh and marine habitats and serve as a vital ecological link between the two realms. One of the major factors that determines the place where different organisms can live within an estuary is the gradient of salt concentration, that is, the salinity. The upper reaches of the estuary are most influenced by the river and therefore may be almost completely freshwater. As one moves downstream the influence of the sea becomes increasingly dominant. The salinity of the water gradually increases until at the mouth of the estuary, it is similar to that of the surrounding coastal ocean.

There are daily changes in the movement of water and the salinity profile within an estuary. At high tide the estuary is flooded with higher salinity seawater, and at low tide the river water may dominate and the flow is in a downstream direction. Seasonal changes in response to times when greater rainfall and snowmelt wash down the rivers also strongly influence the estuary.

Another characteristic of estuaries is the salt wedge. Since saltwater is more dense than freshwater, the saltwater tends to underlie the river water where the two meet. Thus the surface water of the estuary is usually much fresher than that at the bottom.

These changes in salt concentration within the estuary present a real challenge to plants and animals. They not only have to be salt tolerant, but they also have to be able to tolerate changes in salinity, thus estuaries have their own unique species that differ from those of wholly freshwater or marine habitats. Those few plants that have been able to adapt to life in the estuaries, such as seagrasses, salt marsh plants, and different types of algae, are often extremely productive because having adapted to tolerate the stresses of changing salinities, growing conditions are ideal. Intertidal plants, such as salt marsh grasses and mangrove trees, submerged sea grasses, and algae, are constantly moist with a steady supply of nutrients coming from the sea or the river. As a result, estuaries are among the most productive ecosystems on Earth in terms of the amount of organic matter produced by plants and algae. Estuaries are home to abundant fish, bird, and invertebrate populations, which take advantage of this tremendous plant and algal productivity. Many species of ocean fishes, including a number that are commercially important, spend their juvenile stages in the relative safety of estuaries where the abundance of life sustains their growth to adulthood.

Located at the end points of watersheds, estuaries are often sites where pollutants accumulate and thus the estuaries are very sensitive to human activities. Pollutants generated in the watershed and transported downstream by rivers tend to settle out once they reach estuaries. Thus estuaries serve as barometers of the health of entire watersheds.

Coastal Dunes

Coastal dunes are an unstable, shifting habitat whose very structure is a product of ocean currents, winds, and storms. Currents and waves along the shore deposit sand on the beach, then winds shape the sand into series of small hills that often gradually migrate inland to be constantly replaced at the beachfront by new dunes. Winter storms may completely reshape the landscape, blowing holes in the dunes closest to the ocean and starting the process over.

Sand is unstable, which is why dunes can achieve a maximum stature of only several hundred feet. Dune plants have to be able to tolerate life in shifting sands where water rapidly **percolates** through the soil and out of the reach of plant roots. Plants that grow on sand dunes must be able to tolerate harsh, desert-like conditions where, as any beachgoer who has walked barefoot on hot sand will attest, there is no shade and daytime temperatures can be extremely hot. Dune plants have a lot in common with desert plants, in which fresh water loss and overheating are real problems. Thus many are **succulent** or have thick **cuticles** on their leaves and deeply sunken **stomata** to prevent water loss. These same kind of adaptations are found in cacti and other desert plants.

percolate to move through, as a fluid through a solid

succulent marked by fleshy, water-holding leaves or stems

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

stomata openings between guard cells on the underside of leaves that allow gas exchange

The roots of some dune plants play a role in stabilizing sand dunes, helping to shape the nature of this ecosystem. Beach grass is particularly notable in this regard and is often planted deliberately by people to keep dunes in place. The rapidly growing network of roots produced by beach grass penetrates deep into the dune, lending structural support that can keep the dune in place except under the most severe coastal storms. Beach naupaka, a shrub, is valued the same way on Hawaii and other Pacific islands. A dune initially covered by these stabilizing plants is ripe for colonization by other plants, thus the original plant colonizers set the stage for a successional cycle. SEE ALSO Aquatic Ecosystems; Halophytes.

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Coca

Coca plants are the only natural source of the alkaloid cocaine and related compounds. For several thousand years, the leaves of the coca plant have been used by South American Indians as a mild stimulant, a remedy for medical problems, and for ritualistic or religious purposes. Coca chewing reduces hunger and increases endurance. It also eases the nausea, dizziness, and headaches associated with altitude sickness and relieves the symptoms of various stomach ailments. From **pre-Columbian** times coca has been an integral part of Andean cultures, and the commerce of coca leaves is still a legal and accepted practice in Peru and Bolivia.

pre-Columbian before Columbus

The extraction and purification of cocaine hydrochloride from coca leaves, first accomplished in the mid-1800s, yields a drug with very different pharmacological effects than those associated with traditional coca chewing. Recreational use of cocaine produces a quick sense of euphoria

Leaves and fruit of the coca plant.

and heightened awareness. Its use became widespread in the United States and elsewhere in the 1970s. It has since resulted in profound economic and sociological impacts both in the South American countries where it is grown and refined as well as in countries worldwide where it is consumed.

Coca leaves can be harvested several times a year from two shrubby species of the genus *Erythroxylum. Erythroxylum coca* has two varieties, the main one occurring along the lower slopes of the Andes in Ecuador, Peru, and Bolivia, and a lesser-known variety called ipadu in the lowlands of the upper Amazon basin. This is the species grown most intensively for cocaine extraction. *Erythroxylum novogranatense* is a related species that differs slightly in its chemical composition and leaf and floral features. This species, which grows naturally from northern Peru to Colombia, is part of the original formula of Coca-Cola® and is still used today as a flavoring in the popular soft drink (but only after the cocaine is first extracted from the leaves).

In traditional use, coca leaves are dried before they are chewed, and to increase the release of alkaloids, small amounts of lime are added to the **quid** of masticated leaves. In lowland Amazonia, where the alkaloid content is generally lower, a fine powder is made from the leaves and mixed with leaf ashes before being made into a quid. To extract cocaine from coca leaves, a large volume of leaves is required, and they are first soaked and mashed in a series of solvents such as kerosene and sulfuric acid and neutralizers like lime, which results in the **precipitation** of a crude cocaine paste. To produce purified cocaine hydrochloride from the paste, more controlled laboratory conditions are required, using reagents such as acetone, ether, and hydrochloric acid.

quid a wad for chewing

precipitation falling out of solution

Cocaine is most often inhaled through the nostrils, but it can also be smoked as a paste or as crack cocaine, or even freebased using an organic solvent. All of these chemically concentrated forms of cocaine have proven to be highly addictive. From the local growers to the paste producers to the clandestine laboratories, then through the international and local drug distribution networks, cocaine demands a high street price and forms the

illicit illegal

basis of a multibillion-dollar **illicit** economy. SEE ALSO Alkaloids; Medicinal Plants; Psychoactive Plants.

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Coevolution

herbivore an organism that feeds on plant parts

When two kinds of organisms exert natural selection on each other so they influence each other's evolution, they are undergoing coevolution. Any two organisms may exert selective pressure on each other. **Herbivores** exert selection on plants favoring the evolution of defenses, and plant defenses exert selection on herbivores to overcome them. Competitors exert selection on each other favoring superior competitive ability. Pollinating insects exert selection on flowering plants to provide attractants and rewards, and plants exert selection on pollinators for superior pollination service. This reciprocal natural selection is the core concept in coevolution. It may produce ongoing evolutionary "warfare," in which the participants constantly change their weapons or tools, or it may produce a relationship that benefits both participants. When the outcome is beneficial to both, it is called mutualism.

In 1964 entomologist Paul Ehrlich and botanist Peter Raven suggested that these reciprocal changes in physical, chemical, or behavioral traits could be great enough to generate new species. Theoretically, as selection favors changes in each partner, the altered partner could differ from its ancestor enough to become isolated as a new species. For example, if a plant gains protection from its parents' enemies (disease or insects) by producing novel defenses, and if this protection is lost by sharing genes with the parental plant types, then selection should eventually eliminate mating between these two types, resulting in two species where before there was one. Natural selection may then favor enemies capable of colonizing the new plant species, with subsequent reproductive isolation and the formation of additional enemy species. New enemy and plant species are thus formed. Ehrlich and Raven claimed that coevolution may be the major kind of interaction generating the diversity of species on land. While many scientists are skeptical of that statement, the evidence of coevolution is all around us, and many fascinating relationships in nature have arisen from it.

Evidence of Coevolution

Most plants and animals experience natural selection from many sources at once. So it seems unlikely that one organism would be the sole or even the primary selective influence on another. Nonetheless, there are good examples of tightly coevolved relationships (the two participants have a highly specialized interaction). In these cases, the selective advantages gained by responding to one source of selection (the other participant) must outweigh many other factors.

For example, butterflies in the cabbage butterfly family (Pieridae) feed primarily on plants in the cabbage family (Brassicaceae). Members of the cabbage family (cabbage, broccoli, mustards) all share a common set of chemical defenses, called glucosinolates, that are found in very few other plant families. Species in the cabbage butterfly family are capable of feeding on these **toxins** without harm. According to the coevolutionary view, a mutation long ago in a cabbage ancestor provided that plant with the ability to make glucosinolates, which allowed it to escape the pests plaguing its glucosinolate-free ancestors. But soon natural selection favored butterflies with mutations allowing them to feed on glucosinolates, and these butterflies were able to eat the new plants. Additional mutations in the plants produced new glucosinolates, protecting those plants but selecting for butterflies that could overcome the new chemistry, and so on. In the coevolution scenario, the ability to produce glucosinolates and stepwise responses to evolving enemies resulted in the cabbage family as well as the cabbage butterfly family. If we were to draw cladograms, or evolutionary trees, for coevolved insects and their host plants, they would be near-mirror images, since each chemical change and **speciation** event among the plants should have produced one in the insects, and each change in the insects should have produced one in the plants.

toxin a poisonous substance

speciation creation of new species

Factors Inhibiting Coevolution

Closely matched trees are said to be concordant, an indication of coevolution between two sets of organisms. Scientists have thus far found few concordant trees involving plants and insects, for at least four reasons. First, it is very difficult to construct such trees, especially for insects, because the fossil record (and even current knowledge about insect diets) is so incomplete. Diets are not preserved in the fossil record. Second, insect and plant evolution are influenced by many things. Most plants are attacked by many different kinds of enemies, and a single defense is unlikely to work equally well against all. And insect success is dependent not only on food, but on weather, escape from predators and disease, and other factors. So plants may not be the single greatest influence on insects or vice versa.

Third, these selective factors interact. The **susceptibility** of insects to predators, parasites, and disease is also influenced by plant defenses, sometimes in a direction opposite to the way chemistry influences growth and reproduction. For example, gypsy moths grow larger and produce many more eggs when feeding on aspen leaves than on oak. But they are killed readily by a viral disease when they feed on aspen and are protected by oak leaves. So there are conflicting selective forces acting on the insects. The net result is that gypsy moth caterpillars do not distinguish between oaks and aspens consistently. Similarly, plant defenses against their own diseases sometimes inhibit production of defenses against herbivores. This would make coevolution between plants and herbivores very unlikely.

susceptibility vulnerability

Fourth, herbivores usually do not exert enough selection to favor major changes in the plants. They rarely consume more than a small fraction of their plant food and seldom kill plants outright. Compared with other factors, like obtaining water, nutrients, and light, herbivores are seldom the strongest evolutionary influence on plants. Similarly, competitors infrequently exert the kind of influence on plant neighbors that would produce

> **FIGS AND FIG WASPS**
>
> More than nine hundred species of figs (*Ficus*) are pollinated by figs wasps (family Agaonidae) in relationships that exhibit closely coevolved characteristics. The hollow fig inflorescence is formed by a swollen flower receptacle (base) and is lined inside with flowers that go through five stages:
>
> 1. **Prefemale,** in which the fig is closed to wasps as flowers develop;
> 2. **Female,** in which tiny wasps crawl inside the inflorescence through a special pore and lay eggs in the mature flowers;
> 3. **Interfloral,** during which wasp larvae develop inside some female flowers while others produce seed;
> 4. **Male,** in which male flowers mature, producing pollen, while the new generation of wasps emerges from female flowers. Female wasps mate, collect pollen, and exit through escape holes bored by males; and
> 5. **Postfloral,** in which seeds ripen, and the fruit becomes attractive to animals that disperse it.
>
> The escaped females invade new fig flowers on other trees, repeating the cycle. The figs provide specialized flowers in which the wasps lay eggs, sacrificing these as a reward, and the timing of male and female flower production is designed to match the wasps' development. The wasps are specifically adapted for life in the fig, and cannot lay eggs or feed anywhere else. Usually only one wasp species can live in one fig species. A natural consequence of this system is that the figs we eat contain some of the minute wasps that do not escape.

coevolutionary patterns. Plants exhibit adaptations to competition, including growth responses to the green light reflected from neighbors, and perhaps the production of chemicals toxic to competitors (allelopathy). But there are few, if any, clear cases of mutual adaptation among plant competitors.

But diseases do kill plants frequently and so exert strong selection on plants favoring defense responses specific to the attacking microbe. Scientists have documented many gene-for-gene interactions between plants and **pathogens** in which a single gene difference between two plants can determine susceptibility to a given microbe. A single gene difference between two microbes can determine which can successfully attack a given plant. One can clearly see evidence of coevolution in these cases, where plants have responded to pressure from microbes with successive genetic and biochemical modifications and the microbes have responded in kind to those changes. A few similar examples do exist for plants and insects, in plant species (e.g., conifer trees, parsnips) with defenses strongly influenced by genes (and less by environment) and insects that can kill them.

Mutually Beneficial Coevolution

Perhaps the most striking examples of coevolution involve mutualisms, in which the participants have exerted selection that makes their relationship increasingly beneficial to each of them. In mutualisms natural selection has favored traits in each participant that strengthen or improve the relationship and its benefits. These interactions contrast with those described above, in which each organism participates at the other's expense.

For example, insects and other animals that transfer pollen among flowers (pollen **vectors**) provide a crucial service to the plant while receiving a reward, usually nectar and pollen itself. Because it is disadvantageous for a plant's pollen to be deposited on the flower of another species, natural selection has favored the evolution of traits to reduce these "errors," usually by narrowing the range of species attracted and moving pollen. For example, flowers may produce nectar guides, patterns that reflect ultraviolet wavelengths, making them visible only to certain insects. Others may provide a long, tubular entrance accessible only to night-flying moths with long tongues. The length of a flower's corolla tube is often matched to a particular moth having the same tongue length. This ensures that the pollen will be carried only to other flowers with the same tube length, presumably of the same species. Some flowers provide necessary resources for specific insects, such as oils needed to cement a bee's nest or for mating purposes. In each case, there presumably has been a series of evolutionary changes in the flower (such as corolla tube length) that exerted selection-favoring changes in the pollen vector (tongue length, for example), fine tuning the interaction to mutual benefit.

The evolution of mutualism provides opportunities for deception. For example, many species of orchids produce colorful flowers and odors but provide no reward. They depend on mistakes made by inexperienced bees to get their pollen onto a vector. To ensure that a mistake pays off, the orchid is constructed so that any visiting bee necessarily carries away the pollen in sticky packets called pollinia deposited on its body. The flower is constructed so that when the bee makes a second mistake the pollinium is removed and deposited on the stigma of the second flower. Pollen transfer

A parasitic fig wasp (*Torymidae*) inserting its ovipositer into a fig (*Ficus capensis*).

has to be efficient; terrestrial orchids in temperate North America may only be visited once in a decade.

Some tropical orchids improve their chances of being visited by producing volatile chemicals that are collected by certain bees and used as mating signals. Some orchids may produce an odor that mimics a bee's mating signal, attracting bees that are then disappointed in finding no mate, but carry away a pollinium. In more elaborate coevolved interactions the orchid flowers actually look like a female bee or wasp, with which males attempt to mate. In yet others the flower resembles a male bee, and territorial males attack it. In these latter situations, the pollinia are deposited on the bee when it contacts the flower to mate or fight. All of these deceptive floral adaptations produce a very dependable relationship between the plant and insect (pollinator constancy), but at the insects' expense.

Plants may form mutualisms with potential enemies as well. A limiting step in the nitrogen cycle is the capture of inorganic nitrogen from the air and its incorporation into organic forms plants can use. Bacteria have developed this ability, called nitrogen fixation, and are a critical link in this cycle. Legumes and some other plants have formed associations with certain bacteria, particularly the genus *Rhizobium*, in which the bacteria live in swellings, or nodules, on the plant roots. But since many bacteria are enemies (pathogens) of plants, plants and *Rhizobium* have had to reach a coevolved

pathogen disease-causing organism

vector carrier, usually a carrier who is not affected by the thing carried accommodation. Through coevolution, they have developed a specialized interaction that depends on manipulating expression of each other's genes. *Rhizobium* produces signals that turn off plant defense responses and identify it as friendly to the plant. Host plants produce chemical signals that turn on genes in the bacteria that produce signals directing the plant root to produce a nodule. The bacteria then invade the nodule, where the plant provides necessary nutrients in return for nitrogen. It is clear that this relationship has evolved from a battle between enemies, host and pathogen, to a mutualism.

Unanswered Questions

oviposition egg-laying

Scientists are divided about how many species have been shaped by coevolution. Several important questions need to be answered before this issue will be resolved. If insects exert relatively little pressure on plants, how often would plant defenses change? Do insects make mistakes in selecting plants as food or **oviposition** sites? If not, how do they ever begin feeding on a new plant type? How great a change is necessary to provoke a response in the coevolutionary partner; for example, how much change in the shape of an orchid is necessary to provide improved visitation by an insect? And how can we evaluate the importance of the coevolutionary partner versus other factors that influence the evolution of plants, animals, and microbes? SEE ALSO Evolution of Plants; Interactions, Plant-Fungal; Interactions, Plant-Plant; Interactions, Plant-Vertebrate; Pollination Biology.

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Coffee

The coffee plant is a woody shrub native to the understory of the forests of east Africa. The genus responsible for this caffeine-loaded beverage is *Coffea*, to which taxonomists assign between twenty-five and one hundred distinct species. Some 80 percent of the world's coffee comes from *Coffea arabica* L., known as arabica coffee on the global market. Most of the remaining world trade features *Coffea canephora* Pierre ex Froehner, commonly known as robusta coffee. Robustas have about twice the caffeine content found in arabicas.

lateral side

apical meristem the growing tip of a plant

Coffee belongs to the family Rubiaceae, a commercially important family that provides the drugs quinine (*Cinchona* spp.) and ipecac (*Psychotria ipecacuanha*), as well as the sweet-scented ornamental known as *Gardenia augusta*. Like many woody species growing in a forest setting, coffee has a vertical stem with horizontal branches. The **lateral** branches become progressively longer the farther away they are from the **apical meristem**, giving the shrub an overall pyramidal or Christmas-tree shape.

A worker looking for mature coffee beans on a plantation in Java, Indonesia.

Shiny, waxy, dark green leaves occur in opposite pairs. They are elliptical in shape with distinctly visible veins. The underside of leaves, like other species in the family, shows small cavities (domatia) at the midrib/lateral vein junctions. While the function of these domatia remains a mystery, some investigators believe they might serve as "houses" for mites or ants.

Coffee flowers are small, fragrant, white structures with five to nine narrow petals. Flowering usually comes about ten days after the first rain ends the dry season. A blanket of frostlike **inflorescence** and its associated perfume can envelope a large estate for two days before the flowers start to fade. Pollination by bees, wasps, and flies leads to fruit set. The fruit, called a cherry or berry, is actually a **drupe** that turns dark red (or yellow in some varieties) when ripe. It usually contains two seeds (the beans) surrounded by a sweet mucilage.

inflorescence an arrangement of flowers on a stalk

drupe a fruit with a leathery or stonelike seed

Distribution of Coffee Cropping Systems

Coffee production occurs within the confines of the tropics, girdling Earth some 23.5° latitude north and south of the equator. As a mountain-loving shrub, *C. arabica* does best in the temperate climatic regimes associated with high tropical altitudes. Most coffee zones have temperature ranges from 17° to 25°C. But wherever coffee grows close to subtropical latitudes (as in southern Brazil) or in extremely high mountain regions, frost threatens the harvest from time to time. Minimum rainfall for a profitable crop is 1,200 to 1,500 millimeters per year. Excessive **precipitation** (greater than 2,500 millimeters per year) or windy conditions **impede** production by hampering pollination or fruit set.

precipitation rainfall

impede slow down or inhibit

World production of coffee in 1998 exceeded 6.4 million metric tons, harvested on lands covering more than 10.7 million hectares (an area equivalent in size to Guatemala or Bulgaria). Coffee exports derive from more than fifty countries. Though native to east Africa, coffee production has found a solid base in the New World (the Western Hemisphere), where Brazil, Colombia, Mexico, and the Central American countries account for

59 percent of global exports (of all coffees—arabicas and robustas combined). Brazil is the single-largest exporter. Other important producing countries include Ecuador, Peru, and Papua New Guinea for arabicas, and Indonesia, Ivory Coast, Uganda, and Vietnam for robustas.

From Tree to Cup

Processing of coffee beans into the morning habit many people know as having a cup of coffee begins with the harvest. The relatively short interval in which most beans mature requires the mobilization of a large workforce. Men, women, and children alike participate in this annual event. During peak harvest, a family of six might pick 400 to 600 pounds of beans. For every 100 pounds of freshly picked "cherries," workers receive on average the equivalent of $3.33. Once picked, the cherries may be processed in one of two ways: the wet or washed method, in which water is used to wash, ferment, and rewash the beans; or the dry or natural method, in which the fresh bean is left to dry in its husk. The preferred method for the U.S. palate is the wet method.

Once washed and sun dried on patios or in large cylindrical tumbler-dryers (in areas where rain prohibits patio drying), the beans are milled by machines that remove the final thin parchment. Beans are normally dried to about 11 percent moisture content, which inhibits fermentation or molding of the commodity in shipment. Once milled and dry, the gray-green or bluish beans are ready to travel the world to wherever they are to be roasted. The 100 pounds picked for $3.33 mentioned previously, can, if it is quality coffee, fetch anywhere from $6 to $9 per pound in the specialty coffee shops of the United States.

Coffee quality (its taste or "cup quality," as the experts call it) depends upon a host of factors, including soil, climate, altitude, and processing. The best-quality coffees come from mountainous regions where high standards in processing are consistent. The slow growth at higher elevations produces a harder bean, a highly prized quality on the world market. But locale is only one part of the quality equation. Processing plays a critical role in the final product, which means that coffee grown in the best environmental conditions can be transformed into a mediocre commodity if not processed correctly.

Consequences of Different Cultivation Practices

As an understory shrub native to east Africa, *C. arabica* is evolutionarily suited to shade conditions. Many coffee growers today—the majority of whom cultivate small plots in poor rural areas—produce their coffee beneath the shade of taller trees. This traditional, forestlike system, while technically an artificial or managed forest, provides an array of what ecologists call ecological services. The foliage cover intercepts heavy tropical rainfall, lessening its impact upon the soil. The leaf litter generated by the canopy provides a mulch layer that further helps to protect the soil, and gradually decomposes into the soil, recycling the nutrients contained in the leaves and other debris. Shade trees with deep roots draw nutrients from lower soil layers into the system. And a diverse mix of plant species creates a relatively stable ecological system with little need for chemical inputs such as synthetic fertilizers or pesticides.

The shade canopy often includes tree species that are nitrogen-fixing **legumes** (e.g., *Inga* spp., *Albizia* spp., *Gliricidia* spp., etc.), fruit trees such as citrus species, avocados, or bananas, and species that yield precious hardwood (e.g., *Cordia* spp.). This agroforestry management strategy provides noncoffee products that can be used by the farm family or sold on local markets.

legumes beans and other members of the Fabaceae family

Recent changes in production, encouraged by the late-twentieth-century gains in basic grain crops such as corn, wheat, and rice, have changed the coffee landscape in many countries. Higher plant density (number of individual plants per hectare), the use of high-yielding varieties, and the introduction of an array of agrochemicals (fertilizers and pesticides) now characterize a growing number of farms. These changes are often accompanied by a reduction or total elimination of shade trees. In many Latin American countries, fear of the disease known as coffee leaf rust (*Hemileia vastatrix*) and of its spreading in the shaded environment of traditional systems has fueled the transformation from shade to sun or nearly shadeless systems. The objective is to increase yield (production per unit area).

The goal of increased yields is certainly laudable, but it ignores the total production of both coffee and noncoffee products obtained from a traditional, shade coffee system. Noncoffee products such as fruits and firewood, for instance, can represent upwards of 20 percent of a farm's annual income. When shade trees are removed completely or greatly reduced in number, a farmer becomes much more dependent upon the volatile international price of coffee—a position few peasant farmers can afford.

Aside from the socioeconomic impact of changes related to production, there are also some environmental consequences. Obviously, the benefits afforded the soil from the forestlike setting are reduced or lost along with the shade cover. Moreover, recent research shows that shaded coffee lands can play a role as a refuge for biodiversity. Birds use shade coffee lands similar to the way they use natural forests. The important features of the shade are the species diversity of the shade trees (the different types of shade trees) and the structural diversity of the shade trees (the height and layers of the canopy). In fact, from ornithological work conducted in Mexico, Guatemala, and Peru, we now know that coffee managed in a way that maximizes the species and structural diversity of the shade component harbors a bird community as diverse as that found in natural forests in the same region. SEE ALSO AGRICULTURAL ECOSYSTEMS; ALKALOIDS; ECONOMIC IMPORTANCE OF PLANTS; PSYCHOACTIVE PLANTS.

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College Professor

The career of college professor is based on a commitment to lifelong learning. Most college professors in the plant sciences have earned a Ph.D., a degree signifying expertise in a specialized subject area such as agronomy, plant pathology, or molecular biology. An individual wishing to become a professor typically completes four years of college, usually majoring in biology or a related area such as botany, biochemistry, or genetics, and receives a bachelor's degree. This is followed by additional college courses, usually over a four- to six-year period, that result in the Ph.D.

specimen object or organism under consideration

College professors typically have duties involving teaching, research, and service. Most professors teach several courses during the academic year. Some may be introductory courses having hundreds of students, while others may be advanced courses having only a few. Some courses are taught in the classroom where the professor may lecture or lead discussions. Other courses are taught in the laboratory or on field trips, where the professor teaches students to collect **specimens**, operate instruments, make observations, and analyze data. Associated with teaching are related activities such as meeting with students during office hours, preparing lectures, writing exams, and grading student work. In addition, most professors in the plant sciences are expected to do research. This may involve conducting experiments in the laboratory or field, collecting specimens throughout the world, analyzing data using the computer, writing results for publication in professional journals, and working in the library to learn about the work of others. Finally, most professors are expected to perform services such as advising students, serving on college committees, participating in national organizations that focus on teaching or research, and serving as a resource person at the community, state, or even global level.

In the United States, the college professor may work in a community college, a four-year college, or a university. In a community college, a professor's emphasis is on teaching. In a four-year college, the emphasis is usually on a combination of teaching, research, and service. In a university, an institution consisting of several colleges, the emphasis is usually on research.

When a person with a Ph.D. is hired, it is usually at the rank of assistant professor, a temporary position lasting approximately six years. At the end of this period, based on the person's accomplishments in the areas of teaching, research, and service, he or she is promoted to associate professor and receives tenure, a condition that provides employment for life. Based on continuing accomplishments, an associate professor may be promoted to full professor. In 1999 the average annual salary for assistant professors was approximately $42,000, for associate professors $51,000, and for full professors $65,000.

Regardless of academic rank and where employed, college professors frequently mention the ability to interact with students as one of the greatest rewards of their profession. In addition, they enjoy the freedom to conduct research on topics of their own choosing, to make discoveries that contribute to scientific knowledge, and to generally participate in a lifelong learning experience. SEE ALSO Agronomist; Food Scientist; Physiologist; Systematics, Plant; Taxonomist.

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Compost

Compost refers to a biological process that uses any one of several methods to speed up the decomposition of raw organic matter, usually by piling, aerating, and moistening. It is also the crumbly, nutrient-rich product of this process.

Composting is an important means of recycling organic wastes to return their nutrients to the soil, where they become available to plants. Composting reduces or eliminates problems with odors and water pollution from raw waste products such as livestock manure and slaughterhouse and food-processing wastes. Many cities compost yard wastes in order to conserve scarce landfill space. High-temperature composting methods also kill weed seeds and **pathogens,** turning a potentially expensive health hazard into a valuable resource. The resulting product contains balanced soil and plant nutrients, including trace minerals, and is rich in beneficial microbes that further improve the soil's ability to nourish plants. Composed primarily of **humus**, compost also conditions the soil, making it easier to work and improving its drainage, **aeration**, and nutrient holding capacity.

pathogen disease-causing organism

humus the organic material in soil, formed from decaying organisms

aeration introduction of air

Almost anything that was once alive or is a waste product of a living organism can be composted. Dry, bulky materials, including wood products such as sawdust and newspaper, as well as straw, cornstalks, and leaves, contain a high proportion of carbon relative to nitrogen. Materials that are wet, heavy, and smelly, such as manure, grass clippings, and fish wastes, are usually high in nitrogen relative to carbon. Both types of materials should be combined in a ratio of about thirty parts carbon to one part nitrogen to promote thorough decomposition. Mineral powders such as rock phosphate can be added to compost as a source of trace elements, which can also be supplied by organic materials such as seaweed and bonemeal. Microbial cultures and worms are sometimes used to improve compost activity. Large quantities of fats or oils, as well as toxic or synthetic materials, should not be added to compost.

Compost requires enough air and moisture to provide optimum conditions for microbial activity. Turning compost to incorporate more air will speed decomposition, generating higher temperatures. Compost can be finished in anywhere from two weeks to a year, depending on climate, what kinds of materials are used, and how often it is turned. Finished compost has a spongy texture and earthy fragrance, and its original ingredients are no longer identifiable.

Compost can be used as a fertilizer and soil conditioner on any scale, from houseplants to large farms. It contains a good balance of essential plant nutrients in a stable form that will not leach away in the rain, and

A garden compost pile.

can be applied at any time of year without danger of burning plants. Compost can be included in potting soil, spread on lawns, worked into garden beds, side-dressed around trees and perennials, and added to transplant holes. Compost is often used to stimulate growth of new vegetation on land that has been strip-mined or badly eroded. Compost tea can give growing plants a quick boost, and is known to suppress certain plant diseases because of its beneficial microorganisms. Organic farmers rely on compost to build soil fertility and recycle nutrients. SEE ALSO AGRICULTURE, ORGANIC; FERTILIZER; SOIL, CHEMISTRY OF; SOIL, PHYSICAL CHARACTERISTICS OF.

Grace Gershuny

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Coniferous Forests

Coniferous forests are dominated by gymnosperm trees such as pines, spruces, and firs. Conifers were the first plants to evolve seeds. Gymnosperms (from the Greek words *gymnos*, meaning "naked," and *sperma*, meaning "seed") have seeds exposed to the environment on cones. In most species, male and female cones occur on the same tree, but the *Juniperus* (juniper) and *Taxus* (yews) genera have species with separate male and female trees. Male cones are smaller than female cones and produce pollen in the springtime. The larger female cones are able to be fertilized only when they are young and often unnoticeable. Most conifers rely on wind to carry their beautiful and diversely shaped pollen grains to the female cone.

The phylum Coniferophyta is organized into two orders. Older classification schemes included a third, Ginkgoales, containing only one species (*Ginkgo biloba*); more recent classification schemes now place *Ginkgo* into its own phylum, Ginkgophyta. Coniferales, with five families and over six hundred species, including the species most often identified with coniferous forests, is the most populous order. Some of the world's most remarkable plants are found in Coniferales. Bristlecone pine (*Pinus aristata*) can live to be over six thousand years old; coastal redwoods (*Sequoia sempervirens*) grow to be over one hundred meters tall; and Monterey pine (*Pinus radiata*) is one of the most productive timber species. The Taxales order contains two families and over thirty species but is best known for the poisonous yew (*Taxus*) genus.

Conifer Leaves

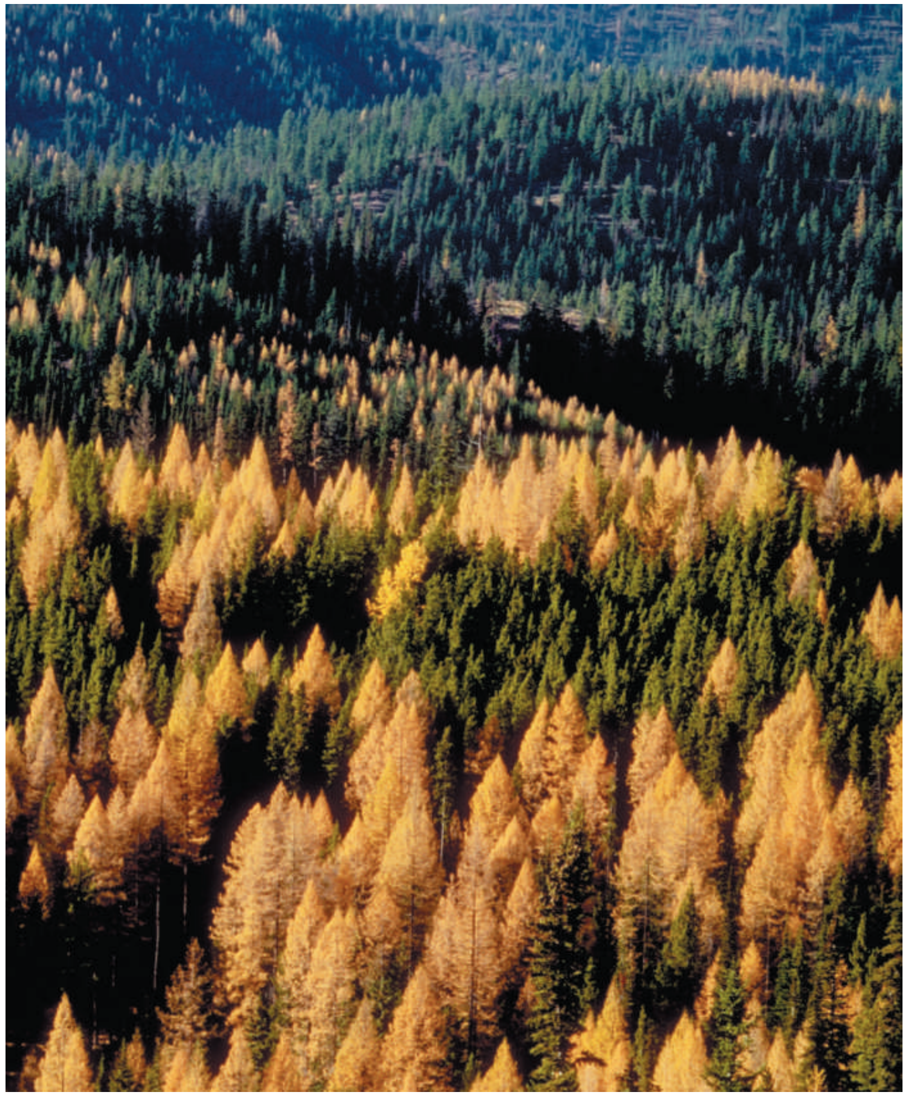
Most conifers are evergreen, meaning that they maintain green leaves, usually needles, year-round. Needles exist in all families. Scalelike leaves often obscuring the woody portion of the shoot exist in the Cupressaceae, Podocarpaceae, and Taxodiaceae families. The Podocarpaceae family contains the only broadleaf conifers. Two genera, the celery pine (*Phyllocladus*, found in the Southern Hemisphere) and the Japanese umbrella pine (*Sciadopitys*), do not contain true leaves and instead carry out photosynthesis using specially adapted shoots.

In climates with mild, wet winters and warm, dry summers, drought adaptations and the ability to conduct photosynthesis all winter give evergreen conifers a distinct advantage over deciduous **angiosperms**. In the boreal forest, conifers succeed due to a combination of factors. First, growing seasons are short and conifers are able to begin photosynthesis with a full canopy as soon as temperatures warm. Second, because needles last from two to ten years, conifers need to replace fewer leaves each year than deciduous trees. Since leaves require large amounts of nutrients, nutrient-poor areas (such as the boreal forest and the southeastern United States) are often dominated by conifers. Third, conifers are more able to resist periodic drought stresses common in the boreal forest. Finally, in climates where temperatures dip below -45°C, conifers can survive where angiosperms cannot.

angiosperm a flowering plant

Nearly all conifers are evergreen but there are four deciduous genera: *Larix*, *Pseudolarix*, *Metasequoia*, and *Taxodium*. The *Larix* and *Pseudolarix* (common name larch) live in the boreal forest. In addition to possessing

Western larches change to autumn yellow amid evergreen fir trees in Washington's Wenatchee National Forest.



good cold-resistance, larches have high photosynthetic rates, flush early in the spring, and use nutrients very efficiently. *Metasequoia*, the dawn redwood, grows well on damp sites. *Taxodium*, the swamp cypress, grows in standing water in the southeast United States and parts of Mexico.

Distribution of Coniferous Forests

Coniferous forests exist in many climates around the world. The Podocarpaceae family is distributed in tropical and subtropical climates in South America and Southeast Asia. Small areas of southern Chile and western Argentina have coniferous *Araucaria* species living with evergreen broadleaf species. Mexico and Central America have pine forests in high elevation mountain ranges. Western North America and Japan support one million square kilometers of coastal coniferous rain forests. With nearly sixteen million square kilometers, the northern latitude boreal forests contain the vast majority of coniferous forest area. The Eurasian boreal forest begins in Scandinavia and extends east in a widening band all the way to the Kamchatka Peninsula in eastern Russia. The forest reaches its northernmost boundary at 73°30′N in Siberia but is usually found no farther north than

68°N. In North America, the eastern boreal forest ranges from 45°N to 55°N; the western forest extends from 55°N to 69°N. Forested areas called **subalpine** forests cover about three million square kilometers in the U.S. Rocky Mountains, mid-elevation areas in the Himalayas, and other temperate mountain ranges.

subalpine a region less cold or elevated than alpine (mountain top)

Coniferous Forests in the United States and Canada

U.S. and Canadian coniferous forests follow a general rule found worldwide: as temperatures cool, species diversity declines. In Alaska and northwestern Canada, the boreal forest is primarily composed of black spruce (*Picea mariana*), white spruce (*Picea glauca*), and larch (*Larix laricinia*). Farther south and in isolated warm northern areas, aspen and birch intermingle. In central Canada, lodgepole pine (*Pinus contorta*), jack pine (*Pinus banksiana*), and balsam fir (*Abies balsamea*) appear. East of the Great Lakes, red pine (*Pinus resinosa*), eastern white pine (*Pinus resinosa*), oaks, and maples are common.

The Rocky Mountains resemble the boreal forest but are distinguished by the presence of subalpine fir (*Abies lasiocarpa*). Engelmann spruce (*Picea engelmannii*) replaces black and white spruce. In the central Rockies, drier regions of the northern Rockies, and high elevations of the southern Rockies, Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) are common. In the southern Rockies, Engelmann spruce remains at higher elevations. Piñon pine (*Pinus edulis*) and Rocky Mountain juniper (*Juniperus scopulorum*) occupy the grassland-forest boundary. Trembling aspen exists throughout the Rocky Mountains.

The temperate rain forest, stretching along coastal North America from northern California to southern Alaska, contains western red cedar (*Thuja plicata*), Douglas-fir, Pacific silver fir (*Abies amabilis*), Sitka spruce (*Picea sithcensis*), and hemlock (*Tsuga heterophylla*). Redwoods (*Sequoia sempervirens*) indicate the southern limit of the temperate rain forest. The giant sequoia (*Sequoia gigantea*), one of the largest trees in world, grows well on the western Sierras in California.

Plant-Animal Interactions

Most conifers do not rely on insects, birds, or mammals to distribute their seeds and therefore have fewer readily observable examples of plant-animal interactions than flowering plants. Nonetheless, insects, birds, and mammals maintain strikingly diverse interactions with the coniferous trees in their habitat.

With few exceptions, insects in conifer forests are pests. Moths and butterflies are highly destructive, as are spruce budworms. All coniferous forests have some level of insect infestation. Vigorous forests use sap and other compounds to defend themselves against insects and are rarely catastrophically damaged. Forests in decline as a result of fire suppression or improper management are much more susceptible to insect outbreaks.

Birds in coniferous forests eat seeds and sometimes inadvertently help to plant trees. The Clark's nutcracker, for example, collects seeds from whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) and brings them to nesting areas up to 45 kilometers away. The birds collect more seeds than they eat and the leftovers germinate. Insect-eating birds such as chickadees, nuthatches, and woodpeckers help to control insect populations. Owls and hawks live in coniferous forests and many, such as the spotted owl, use dead coniferous trees for nesting sites.

Mice and squirrels are the most common mammals in the coniferous forest. During the summer, these animals eat buds, berries, seeds, and even bark. Squirrels plan ahead for winter by collecting cones. As with birds not all the seeds are eaten, and some germinate into new trees. Deer, elk, mountain lions, bears, and other large mammals found in coniferous forests do not consume significant amounts of seeds or foliage. By chewing completely around a tree, porcupines interrupt the flow of sugars from leaves to roots. They are the only mammal besides humans known to kill coniferous trees.

Natural and Human-Managed Coniferous Forests

Coniferous forests exist along a gradient from purely natural to purely human created. The boreal forest, because it is so inhospitable and often contains commercially undesirable trees, contains the largest natural coniferous forests. Wildfires, insect outbreaks, and other disturbances are usually uncontrollable in remote boreal forests. In these forests, there is a variety of tree and undergrowth species; abundant animal, insect, and microbial life; and a natural fire cycle.

For most of the twentieth century the U.S. Forest Service pursued a policy of total fire suppression. Without fire, open stands of ponderosa pine were invaded by dense thickets of Douglas-fir and lodgepole pine. Insect outbreaks became common and fuels began to accumulate on the forest floor. Unmanageable and devastating fires such as the 1988 Yellowstone National Park fire caused a shift in public and scientific opinion; forest managers began to reincorporate fire through controlled burns and forests are now beginning the long process of regaining their natural relationship with fire.

In plantation forests, timber companies are interested in producing the maximum possible amount of commercial timber, not maintaining a diverse forest community. Many areas are planted with a single species at the same time. Conifers such as Monterey pine and slash pine (*Pinus caribaea*), because they grow straight and quickly, are popular plantation trees. The lack of species diversity and geometrical forest arrangement make plantations very different from natural or partially managed forests. Plantations do not support diverse **ecosystems** nor are they are desirable for recreation. Society, however, has a large demand for forest products and maximizing plantation production reduces the need to exploit other forests. SEE ALSO BIOME; CONIFERS; DECIDUOUS FORESTS; ECOLOGY, FIRE; FORESTER; FORESTRY; GINKGO; SEQUOIA; TREES.

ecosystem an ecological community together with its environment

Michael A. White

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Conifers

Conifers are the largest, most widespread, and most economically important group of gymnosperms (nonflowering seed plants), including about 630 species divided into six or seven families. Conifers are the oldest extant group of seed plants, dating back to more than 280 million years in the fossil record. Some of the current families and genera have long fossil records; for example, remarkably well-preserved and modern-appearing cones of the genus *Araucaria* dating to 160 million years ago have been discovered, and a well-preserved fossil pine cone dating to 130 million years ago can be compared directly with cones of living pine trees.

Conifer Diversity

All conifers are woody plants, mostly trees or sometimes shrubs. Typical conifers such as members of the pine, cypress, and araucaria families are recognized by their woody seed cones, with flattened or shield-shape cone scales arranged spirally or in pairs or **whorls** around a central axis. The woody-coned conifers usually have winged seeds that are dispersed by wind and gravity. Other important groups of conifers such as the yew family, junipers, and most of the podocarp family have their seed cones reduced to one- or few-seeded fleshy structures that are dispersed by birds. Conifer seed cones range from less than 1 centimeter in length to up to 50 centimeters long and may be quite massive in some species of pines and araucarias.

whorl a ring

Most conifers are evergreen, but a few genera (notably bald cypress, dawn redwood, and larch) shed their leaves during the winter. The majority of conifers have narrow, needle-shaped leaves, arranged in spirals or sometimes in pairs, or are found in tightly clustered whorls on short branches. Pines are unusual in having their leaves extremely tightly clustered in needle clusters (fascicles) with almost no stem elongation between the leaves. Some conifers have their leaves very reduced and scalelike (most of the cypress family), while subtropical to tropical conifers in the podocarp and araucaria families may have the leaves flattened and are relatively broad.

Conifers include some of the longest-living, tallest, and most massive trees in the world. Bristlecone pines from the southwestern United States are among the longest living individual trees in the world, having been dated from tree rings to more than five thousand years in age. Sequoias are among the tallest trees in the world, reaching more than 110 meters in height, while the related giant sequoia reaches 106 meters in height and up to 11 meters in diameter. Large and ancient **specimens** of conifers are featured attrac-

specimen object or organism under consideration

SELECTED CONIFER GENERA

Common Name	Generic Name	Family of Species	Number of Species (approximate)	Geographic Range	Economic Uses
Pine	*Pinus*	Pine	110	Northern Hemisphere	Timber, paper, resins, ornamentals
Spruce	*Picea*	Pine	40	Northern Hemisphere	Timber, paper, ornamentals
Fir	*Abies*	Pine	50	Northern Hemisphere	Timber, paper, resins, ornamentals
Hemlock	*Tsuga*	Pine	10	Eastern and western North America, eastern Asia	Timber, paper, ornamentals
Douglas-fir	*Pseudotsuga*	Pine	6	Western North America, eastern Asia	Timber, paper
Juniper	*Juniperus*	Cypress	50	Northern Hemisphere	Wood, pencils, flavorings, ornamentals
Cypress	*Cupressus*	Cypress	13	Western North America, Eurasia	Ornamentals
Bald cypress	*Taxodium*	Cypress	2	Eastern United States to Central America	Timber, ornamentals
Sequoia	*Sequoia*	Cypress	1	California to southern Oregon	Timber, ornamentals
Yew	*Taxus*	Yew	10	North America, Eurasia	Ornamentals, medicinal alkaloids
Araucaria	*Araucaria*	Araucaria	18	South America, South Pacific	Timber, ornamentals
Podocarpus	*Podocarpus*	Podocarp	95	Southern Hemisphere, northern to eastern Asia, Mexico, Caribbean	Timber, ornamentals

tions in national parks in many parts of the world, most notably sequoias and giant sequoias in California, alerce (*Fitzroya*) in Chile and Argentina, and kauri (*Agathis*) in New Zealand.

Conifer Distribution

Conifers are important forest components in many areas of the world, and members of the pine family are especially abundant in cool to cold-temperate and mountainous areas of the Northern Hemisphere, where such genera as pines, spruces, firs, and hemlocks often form dense forests. Junipers and pines are also very abundant trees in semiarid environments of the Northern Hemisphere such as the Great Basin region of the western United States. Pines are the most widely distributed genus of trees in the Northern Hemisphere and are also especially widely planted as timber trees in both hemispheres.

Several genera of conifers with only a single living species of very restricted distribution were once much more widespread in the fossil record and have been termed "living fossils." These include the dawn redwood (*Metasequoia*) from China and the sequoia and giant sequoia from California. Another remarkable genus, *Wollemia* (from the araucaria family), was known only as a fossil from Australia until 1994, when a living plant of this species was discovered growing in a remote canyon area near Sydney, Australia.

Economic Uses

Conifers are extremely important economically as sources of lumber and other wood products, and are also widely planted as ornamental trees and shrubs. The most important sources of softwood lumber in the world are

A giant alerce tree dwarfs a man near Puerto Montt in the Lake District of southern Chile.

trees in the pine family, especially species of pine, spruce, larch, and Douglas-fir, which are widely used for dimensional timber for building construction and boat building, and for general construction uses such as utility poles, doors, and cabinetry. These woods are also widely used for plywood and veneer and as sources of wood pulp for paper and cardboard and other modified wood products, such as charcoal. Southern yellow pines, such as slash pine and loblolly pine, are widely grown in their native southeastern United States as sources of lumber and pulp, while the Monterey pine from coastal California is now widely planted as a commercial timber tree in the Southern Hemisphere. Douglas-fir (*Pseudotsuga menziesii*) is a particularly important timber species in the northwestern United States and Canada. Several species of pines are tapped or cut and steam-distilled for stem resins, which are used as commercial sources of turpentine, tar oils, rosin, and pitch. Wood of the Norway spruce and white spruce has also been prized for constructing musical instruments such as violins, and the light, strong wood of Sitka spruce has been used for aircraft construction. The attractive reddish-colored wood from species of the cypress family, such as the sequoia, is quite weather- and decay-resistant and is highly prized for building construction, decks, fences, and other outdoor uses. Wood of the western red cedar (*Thuja plicata*) has been heavily used for weather-resistant roof shingles. Fragrant wood from junipers has natural insect-repellent properties and is used for moth-resistant cedar closets or chests. Wood of juniper and incense cedar has been commonly used to make pencils.

Many species of conifers are grown as ornamentals, and a wide variety of cultivated shrub forms have been selected for garden use from members of the yew and cypress families, including several species of yew, juniper, cypress, and golden cypress (*Chamaecyparis*). Conifers from a number of genera are prized as ornamental trees, of which some particularly attractive examples are the blue spruce (*Picea pungens*), the Himalayan cedar (*Cedrus deodara*), and the Norfolk Island pine (*Araucaria heterophylla*). Several species of firs and pines are commercially grown and cut as Christmas trees, and young plants of the subtropical Norfolk Island pine are grown for indoor use as living Christmas trees. Several species of pines from Eurasia and North America are highly esteemed as sources of oil-rich edible seeds (pignoli or pine nuts). Cones of *Juniperus communis* (juniper berries) are used as flavorings in cooking and provide the aromatic flavoring of gin, whose name is derived through the Dutch *jenever* from the name of juniper. Recently, bark and leaves of several species of yews have become important as the source of taxol and related alkaloids, which disrupt the process of cell division and are used in the treatment of several types of cancer. SEE ALSO CONIFEROUS FOREST; EVOLUTION OF PLANTS; FORESTRY; GYMNOSPERMS; SEQUOIA; TREES; WOOD PRODUCTS.

Robert A. Price

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Valerius Cordus.

Cordus, Valerius

German Botanist
1515–1544

Valerius Cordus was an early sixteenth-century German botanist who advanced the study of pharmacology by studying botany in a newly observant way. Born in 1515 as the son of botanist Euricus Cordus, Valerius Cordus was introduced to botany at an early age. He trained with his father and with an uncle who was an apothecary (druggist). In the early 1500s, plants were the main source of medicines used to treat human ailments, and the study of medicine required knowledge of botany. Cordus not only learned botany rapidly from his family, but made brilliant botanical observations of his own. He received his bachelor's degree at the age of sixteen in Marburg, Germany, and went on to study at Wittenberg University. He gave several lectures and wrote a number of important works that were published after his death. Unfortunately, Cordus died of fever in Italy in 1544 at the age of twenty-nine.

By the time of his death, Cordus was already well respected, known for his inventiveness in teaching botany. Rather than relying on just the standard botany in older texts, he made a point of lecturing using examples from his own fieldwork. It was his keen attention to detail in the field that allowed Cordus to write one of the first systematic accounts of herbal and botanical knowledge. Regarding herbals, Cordus gave each plant a full and clear description so that it might be identified without the use of illustrations. He followed a pattern in his descriptions, which was not often the case with other herbals at that time. He included information about the plant stems and leaf arrangements, the structure of the flowers and the time of flowering, and details about the fruits of the plants—and was able to do this despite a lack of descriptive botanical terminology. Cordus included details about the number and types of parts in the flowers and tried to give information about the appearance, smell, and taste of the plants, as well as where they might be found, in an attempt to minimize confusion and mistakes in naming and using herbs at the time. He included information in his works about the ways to derive medicines from the plants he described. After his death, his text became the standard for pharmacy in Germany.

Cordus's attention to detail helped him make great strides in plant taxonomy. Many of his observations and techniques anticipated work done hundreds of years later. Using flower parts to describe and classify plants is still an important taxonomic technique. SEE ALSO CANDOLLE, AUGUSTIN DE; MEDICINAL PLANTS.

Jessica P. Penney

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Cork

Anatomically, cork is a secondary tissue formed from a specialized **lateral meristem** located in the stems and roots of woody gymnosperms and **angiosperms**. The tissue develops from a ring of meristematic cells (the cork cambium or phellogen) located beneath the outer surfaces of the tree, and to the outside of the vascular cambium. The cells that form from the cork cambium are specialized, in that their cell walls contain a high proportion of suberin, a fatty material that **impedes** the movement of water. As cells derived from the cork cambium continue to grow, they eventually die when mature, not unlike the development of xylem cells from the vascular cambium. The result of this process is that the stem (trunk) or root of the tree develops a waterproof covering, generally known as bark. During active phases of tree growth, bark protects the tree from excessive water loss due to the suberized cork cells it contains. Additionally, bark provides a measure of physical protection from direct damage of the tree's trunk by nonliving structures (such as rocks), animals, and humans. In some trees that

lateral away from the center

meristem the growing tip of a plant

angiosperm a flowering plant

impedes slows down or inhibits

Cork strippers harvest the cork of a large cork oak in Portugal.

occur in habitats prone to frequent fires (e.g., savannas, certain coniferous forests), the bark is extremely important to protect the tree against heat damage by providing a layer of thermal insulation between the lateral meristems (vascular cambium and cork cambium) and the outside environment. The insulation properties are due to the cellular structure of cork; the spaces inside the dead cells are filled with air, and this provides resistance to heat flow through the cork.

abrasion wearing away through contact

Several other physical characteristics make cork a unique material. Cork is inherently resistant to **abrasion** and can withstand very high pressures of compression without suffering physical damage. When the pressure is released, the cork returns to its original shape and is seemingly unaffected by the structural changes of compression. Due to the air in its cell spaces, cork is also a lightweight buoyant material, floating easily on water and resisting waterlogging due to its suberized cell walls.

The properties of cork derived from the bark of certain trees has been used by humans for thousands of years. Specifically, the outer bark of the cork oak, *Quercus suber* (family Fagaceae), is the species upon which commercial cork production is dependent. The cork oak is native to the Mediterranean region of southern Europe, and is grown commercially in Portugal and Spain. It is an evergreen oak species, and individual trees have been reported to be in cultivation and are harvested for their bark for periods of 150 years or more.

Production and Harvest

The first cutting of cork oak trees takes place when the trees are between fifteen and twenty-five years old, and produces virgin cork, which is of lesser quality than the cork that develops in the years following the initial cutting. While removing the bark/cork layer, harvesters must avoid damaging the cambial layers beneath the accumulated outer tissues. The first cutting (virgin) cork is not discarded. Some virgin cork is used in the horticultural industry as a growing **substrate** for epiphytic plants, such as bromeliads, orchids, and certain ferns. The waterproof nature of the virgin cork, as well as its rough surface and resistance to decay, provides a long-lasting, natural medium onto which the epiphyte's roots may attach. The virgin cork is also ground up into small pieces, mixed with fillers, adhesives, and other materials to be manufactured into a variety of materials. Subsequent strippings of cork harvests are done at eight to ten year intervals. Each successive stripping causes the production of better quality cork in the next harvest. The trees do not seem to be negatively affected by this harvesting practice when done by experienced cork cutters.

substrate the physical structure to which an organism attaches

Processing

Once the cork has been removed from the trees, the material is washed in water to remove debris and to keep the cork supple for further processing. It can be flattened into sheets and is generally cut to uniform thickness. Depending upon which product is being manufactured, the order of cutting and sizing the pieces may vary. Bottle stopper corks, such as those used by the wine industry, must be of excellent quality and have the properties of uniformly small cell size, uniform suberization and water repellancy, and favorable properties of resiliency. In use, the wine cork is compressed into the neck of the bottle, where it expands and provides an airtight seal; the wine bottle must be stored on its side to keep the liquid wine in contact with the cork in order for the cork to remain moist and maintain the seal. Some wines stored in this manner are useable for over one hundred years. Certain wine experts also feel that over time, the cork imparts certain subtle and desirable characteristics to the flavor of some wines.

Uses

In addition to the familiar uses of cork to close bottles of beverages, cork has a wide range of other uses by humans. It has historically been used as soles of shoes since Grecian and Roman times. Its buoyancy characteristics have been exploited for use as floats for fishing nets, buoys, flotation ballast in small boats, decoys, life preservers, fishing lures, and bobbers for line fishing. Prior to the development of specialized plastics, cork was used in the manufacture of artificial limbs due to its favorable structural characteristics, carvability, and light weight. It also has been used extensively in the preparation of wall coverings and flooring, as cork may have favorable acoustic characteristics, such as the ability to absorb sound, thus reducing noise. In addition, the sealing and insulating properties of cork are used by the automotive and other industries for the manufacture of gaskets. Cork is also frequently found as the surface material in bulletin boards as a prepared composition veneer material made from ground cork particles (often from the first-cut virgin cork, or from lower quality cork harvests). It is used for this application because of its self-healing properties when tacks, staples, or other items are pushed through it and are then removed. Cork is a renewable plant-derived resource and despite advances in wood technology, it continues to be grown, harvested, and used in a way similar to its production and utilization hundreds of years earlier. SEE ALSO Alcoholic Beverages; Ecology, Fire; Trees; Wood Products.

Robert S. Wallace

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Corn

Corn, Indian corn, or maize is one of three grasses that account for almost half of all human calories consumed. The seed of these grasses are called cereals and each developed in a distinct part of the world: corn in the Americas, specifically Mexico/Guatemala (where its name is derived from the Arawak-Carib word *mahiz*, when Christopher Columbus first encountered the grain on the island of Cuba), and wheat and rice in the Old World. Corn was and still is the most important food plant for the indigenous people of the Americas. Its cultivation stretched from the Gaspé Peninsula of eastern Canada to Chile in South America. It is grown from sea level to elevations of ten thousand feet in the Andes.

Origin of Corn

hybrid a mix of two species

Most of the corn grown in the developed world is from improved **hybrid** seed while subsistence farmers plant mostly open-pollinated farmer-selected varieties called landraces. There are approximately three hundred landraces of corn, each with its own geographic/climatic zone where it is most productive. Even commercial hybrid corn in the United States belongs to a recognized landrace, which is called Corn Belt Dent.

Three distinct views on the origin of corn exist within the scientific community: 1) corn evolved from an extinct wild corn, 2) corn evolved from its closest relative, teosinte, and 3) corn evolved after hybridization of either wild corn or teosinte with a more distant relative in the genus *Tripsacum.* During the 1960s there was widespread support for the idea of wild corn as the ancestor of the **domesticated** form. In contrast, in the 1980s the theory holding greatest currency was that of teosinte as the **progenitor** of corn. Recent research suggests that *Tripsacum* has had a role.

domesticate to tame an organism to live with and to be of use to humans

progenitor parent or ancestor

ecosystem an ecological community together with its environment

escarpment a steep slope or cliff resulting from erosion

Although there are distinctly different hypotheses regarding the ancestry of corn, all agree on the basic circumstances surrounding its origin. The **ecosystem** that gave rise to corn had almost frost-free, seasonally dry winters alternating with summer rains, and highland (above 1,500 meters). Sometime between 5000 and 3000 B.C.E., corn appeared in Mesoamerica (Mexico and Guatemala), most probably along the western **escarpment** of south central Mexico in an arc within five hundred kilometers of present-day Mexico City. This location also describes the major area occupied by the closest relatives of corn, both annual and perennial teosinte, and nu-

A farmer checks an ear of corn for ripeness at harvest time in Merti, Kenya.

merous species in the genus *Tripsacum*. Corn and teosinte are unique among the grasses because the male and female flowers are borne in separate structures: the ear, or female seed-bearing cob, is carried half way down the stem while the male central spike, or tassel, is at the top of the stem. In the early stages of domestication the ear was small (one to three centimeters) yielding no more than fifty small, hard, popcornlike seeds. Archaeological corn remains, from cave sites dating back to 3000 B.C.E. in Tehuacán, Mexico, match the above description perfectly. In contrast, modern corn yields a massive ear (25 to 30 centimeters) producing more than 750 seeds. This modern corn plant is unable to disperse its seed because of the unique husk and cob structure where the seed do not fall free at maturity as in all wild plants. Humans must harvest, shell, and plant the seed for maize to exist.

Modern Corn

Modern corn is a single species, *Zea mays*, with five kinds of seeds based primarily on the storage starch of the **endosperm**. The earliest corns were popcorn types with a hard protein rind that held moisture in the starch, and when heated they exploded. Seeds that have a soft starch are called flour corns; sugary varieties are called sweet corn, which are often eaten immature when the sugar content is highest relative to starch; hard-starch varieties are called flint corn; and dent corn, which is intermediate between flour and flint, has a characteristic small dent or dimple at the top of the kernel. Dent corn is the most common form grown in the Corn Belt of the United States (accounting for one-half of the world's total production, valued at fifteen bil-

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

lion dollars). On commodity markets it is called #2 yellow dent. Much of this goes into animal feeds or is used in the chemical and processing industries.

Corn seed is used industrially to make ethyl, butyl, or propyl alcohol; acetaldehyde; acetone; glycerol; and acetic, citric, or lactic acids by fermentation then distillation. Wet milling produces zein, a protein used to make polyurethane, corn starch, and specialty corn products such as high fructose corn syrup (widely used as a sweetener and replacement for sucrose or cane sugar in candies and baked and processed foods).

In the Americas (excluding the United States and Canada) corn is the mainstay of the diet and the preferred cereal. This is also true for east Africa, south Africa, and regions around the Mediterranean and southeastern Europe. More than half of the dietary calories in both Guatemala and Kenya are accounted for by corn alone. In Mexico corn is eaten in tortillas (an unleavened, griddle-toasted flat bread), tamales (dough steamed in corn husks and often stuffed with meat and chilies), *atole* (roasted, ground corn flour beverage) or *elotes* (roasted or steamed ears). In the southern United States it is consumed as grits (boiled, cracked endosperm from which the bran and embryo or germ have been separated), hominy (entire kernels soaked in lye, then washed and boiled). Corn on the cob and corn chips are eaten nationwide. Cornflakes, invented in the United States, are made from toasted rolled grits; they started the boxed cold cereal breakfast a century ago. Popcorn is both an ancient form of consuming corn and a modern one as it comes freshly popped from the microwave. In Andean countries corn is fermented by first a salivation process to convert starch to sugar and then fermentation by yeast to produce *Chicha*. *Pombay* beer is made from corn in Africa; whiskey made from corn is called bourbon whiskey.

Corn kernels or seeds are much larger than either rice or wheat but on a per-weight basis the three supply approximately the same energy as measured in calories. Corn has less protein than wheat and is deficient in the essential amino acids tryptophan and lysine. In the ancient civilizations of Mesoamerica this deficiency never appeared because corn and beans were eaten together and the combination formed a complementary protein supplying all the essential amino acids. Only when corn alone forms a major part of the diet, as in diets of poverty, do we see malnutrition. The corn kernel, especially the germ or embryo, is rich in oil and the grain is a good source of the B vitamins except for niacin. The low content of niacin can lead to the deficiency disease pellagra, historically prevalent in the South until the 1930s and still common in parts of Africa where corn is consumed. Corn grain is an outstanding feed for pigs, cattle, and chickens; the entire plant cut up and made into **silage** is a major food for milk cows. Americans consume much more corn as pork, beef, eggs, and milk than we do from corn products directly. Corn is the largest harvest in the United States and the most valuable crop, but it is also Mexico's most significant gift to the world. SEE ALSO Agriculture, History of; Agriculture, Modern; Economic Importance of Plants; Fertilizer; Grains.

silage livestock food produced by fermentation in a silo

Garrison Wilkes

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Cotton

Four species of cotton are grown for commercial fiber (lint) production. *Gossypium arboreum* L. and *Gossypium herbaceum* L. are grown in Africa and Asia. These produce lint of inferior quality. *Gossypium barbadense* is grown commercially in limited parts of the world and produces a lint of excellent quality, long and strong, that is used in high-quality garments. It is difficult to produce and is grown in limited quantities. *Gossypium hirsutum* is grown on most of the world's cotton acreage, producing a good quality fiber that is shorter and has less fiber strength than *G. barbadense*. The United States, India, China, Brazil, and Australia are major producers.

Cotton is unique since the fiber is an extension of cells of the seed coat instead of being derived from other plant parts, as flax and the other fiber crops are. Each cotton fiber is actually a single cell and is nature's purest form of cellulose. Unlike synthetic fibers, which are made from petroleum, cotton is a renewable resource. The fiber is used in textiles, high-quality paper, cellophane, and plastics. The seed and fiber (seed cotton) are harvested and processed in a gin where the fiber is removed from the seed. The seed

Farm machines harvest cotton in a Mississippi field.

Puffs of cotton grow on the stem of a cotton plant in Mississippi.

is sold for livestock food for ruminant animals such as cattle. Seed is also processed to produce cottonseed oil for cooking and the meal is used as a source of protein for livestock. The fiber is graded for trash content, color, length, strength, and coarseness and generally sold to textile mills.

Before the invention of the cotton gin, the lint was so expensive due to the labor required to remove the lint from the seed that cotton garments were only for the very wealthy. With the invention of the gin, cotton became affordable for everyone. Cotton is a very labor-intensive crop. Slave labor was the principal means of production in many areas until more of the production steps were mechanized.

The cotton plant is a perennial tree that is grown as an annual plant since it is easily killed by freezing weather. The perennial nature of the plant makes it very difficult to grow. The crop can grow too large under good conditions and growth must be controlled with chemicals. The crop in many areas is killed with chemicals in order to facilitate harvest before adverse winter weather develops. Many of the production areas have serious insect problems requiring the use of several applications of insecticide. These problems made cotton one of the first plants to be a candidate for genetically engineered (manmade) insect-resistance genes to be incorporated in order to reduce the use of insecticides. The engineered resistance has been a tremendous success.

A specialty market exists for organically grown (produced without use of chemicals) cotton and naturally brown or green-colored lint. A very small acreage of organically grown cotton is being produced; production, however, is difficult due to severe weed and insect problems. Lint that is naturally white, brown, or green can be produced. The colored lint eliminates the need for artificial dyes. SEE ALSO AGRICULTURE, MODERN; ECONOMIC IMPORTANCE OF PLANTS; FIBER AND FIBER PRODUCTS.

Bobby J. Phipps

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Cotyledon

See Dicots; Monocots; Seeds.

Creighton, Harriet

American Botanist
1909–

Harriet Baldwin Creighton is a geneticist who helped prove that genes are located on chromosomes. She was born in Delevan, Illinois, on June 27, 1909. She attended Wellesley College in Massachusetts and received her Bachelor of Arts degree in 1929. That year she matriculated at Cornell University as a botany graduate student and a laboratory assistant in botany. At that time Barbara McClintock, who later became a top American plant geneticist and Nobel Prize winner in medicine in 1983, was an instructor at Cornell. The two women immediately became friends and began working together on an important genetic problem: since the beginning of the twentieth century, **cytologists** theorized that chromosomes carried and exchanged genetic information to produce new combinations of physical traits, but cytological evidence to prove their hypothesis was lacking.

cytologist a scientist who studies cells

McClintock had bred a special strain of corn (*Zea mays*) with a ninth chromosome that produced a waxy, purple kernel. In the spring of 1930, Creighton and McClintock planted the kernels from this strain. That summer they fertilized the silks with pollen from a plant of the same strain that did not have either waxy or purple kernels. Once the ears were harvested in the fall, Creighton and McClintock found that some of the kernels were waxy and purple and others had inherited one trait or the other—either waxy or purple—but not both, indicating that the two genes had become separated.

When Creighton and McClintock examined the chromosomes of the new kernels under a microscope they saw that the chromosomes had crossed-over, or exchanged segments. They thus proved that genes for physical traits are carried on chromosomes. This process is extremely complex, and cytologists had been working to understand it for more than thirty years. Creighton and McClintock were the first to provide cytological evidence in plants that proved corresponding segments of genetic material on the chromatids of homologous chromosomes are able to cross over during meiosis. They published their remarkable findings in the Proceedings of the National Academy of Sciences, "A Correlation of Cytological and Genetical Crossing-over in *Zea mays*."

physiology the biochemical processes carried out by an organism

Creighton completed her Ph.D. in botany at Cornell in 1933. She went on to teach at Connecticut College as assistant professor of botany in 1934 where she remained for the next six years. In 1940 she accepted a position as an associate professor of botany at Wellesley College in Massachusetts. Creighton's professional career is graced with many distinguished honors. She was twice a Fulbright Lecturer, once in genetics and plant **physiology** at the University of Western Australia and the University of Adelaide in 1952 and 1953, and again in genetics at the University of San Antonio Abad, Peru in 1959 and 1960. Creighton was the first female secretary of the Botanical Society of America (1950–54); she also served as vice president in 1955 and president in 1956. In addition Creighton was a fellow of the American Association for the Advancement of Science (AAAS) where she served as vice president of the Botanical Sciences Section in 1964. Throughout her professional career, she continued to work in the field of plant genetics; much of her research focused on problems of heredity in corn, but her later research sought to investigate the "mad begonia," *Begonia phyllomania*, with its strange growth patterns, which Creighton believed might hold important clues for cancer researchers. She retired from Wellesley College in 1974. SEE ALSO CORN; MCCLINTOCK, BARBARA.

Mary Anne Andrei

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Cultivar

Horticultural plants of the same species that are distinctive enough to be given a name are called cultivars, which is short for "cultivated variety." A cultivar can be distinguished from other similar cultivars by some combination of characters, including appearance, color, taste, size, and pest resistance. Although the terms variety and cultivar are used interchangeably, cultivar is not the same as a botanical variety, which is a taxonomic category below the species level that can apply to both wild and cultivated plants.

According to rules for naming plants, cultivar names must be in modern languages and not italicized. The first letters are capitalized and the name is either preceded by the abbreviation cv. (cultivar) or is put in single quotes. For example, a commonly grown yellow tomato is *Lycopersicon esculentum* cv. Yellow Pear and a popular type of sweet corn is *Zea mays* 'Silver Queen.' Cultivar names can follow generic, specific, or common names.

New cultivars are usually developed from either wild ancestors or established cultivars through selective breeding, a process that has been ongoing since the domestication of plants. Desired traits can also arise through mutations and plant viruses. Modern technologies of cloning and tissue culture that allow plants to be **propagated** vegetatively have added greatly to the number of such cultivars now produced. SEE ALSO Breeding; Horticulture; Ornamental Plants; Species; Taxonomy.

Sue Thompson

propagate to create more of through sexual or asexual reproduction

Curator of a Botanical Garden

The curator of a botanical garden is the person who oversees the operation of the entire facility. He or she is involved in all aspects, including collection, preservation, and education. The successful curator of a botanical garden will have the opportunity to develop major plant collections. Unique plant collections may be obtained through plant expeditions or by exchanges with other botanical institutions and collectors. Field collecting is encour-

Brian M. Lamb, a botanical specialist and the curator of the Alameda Botanical Gardens in Gibraltar, clears water lilies from a pond.

aged and the curator must have travel flexibility. A curator will interact with a talented staff and will meet interesting colleagues from many perspectives.

The curator is responsible for the maintenance, development, and control of all collections, including living collections and herbarium and spirit-preserved collections. The curator is also responsible for periodic review and maintenance of garden design in the context of an overall plan. Specific duties include:

- overseeing periodic review of live plants for damage or disease and general health, taking appropriate measures for improved health
- overseeing periodic inventories to assess losses as well as to guide new acquisitions
- overseeing periodic review of plant labels and making needed repairs or replacements
- maintaining databases for all plant **accessions**, preferably linking both preserved and living collections
- reviewing the development of the garden facilities both to assure the well-being of the collections and to plan for growth
- periodically reviewing the health of herbarium collections, guarding against damage by insects
- seeing that loans of **specimens** to and from institutions are handled in a professional manner
- periodically checking specimens preserved in spirits for loss of fluid, topping vials when necessary
- interacting with the garden director and administrative staff to assure adequate staffing and resources for collections management.

accession a plant that has been acquired and cataloged

specimen object or organism under consideration

The curator is expected to work among both spirit- and herbarium-preserved specimens as well as inside greenhouses and on the grounds and should be able to lift fifty pounds.

The successful curator must demonstrate a love of living plants, plant collections, and people, as well as have expertise in living and preserved collections management. Computer skills in database management, word processing, and grounds collections management through computer-aided programs are required. A master's degree in the organismal plant sciences is preferred, with emphasis on both botany and horticulture. Salary range is commensurate with experience. Salary advancement is accomplishment-based with annual reviews. SEE ALSO Botanical Gardens and Arboreta; Curator of an Herbarium; Herbaria.

Margaret D. Lowman

Curator of an Herbarium

An herbarium is a collection of preserved plants used for research. The job of a curator of an herbarium is to coordinate the growth of the herbarium while preserving the past collections. Depending on the size of a facility the curator may supervise a small or large staff, thus the salary range is great:

approximately $25,000 to $80,000 or more per year. A curator also assists herbarium users and researchers and conducts her/his own research. Most curators of large herbaria have doctorate degrees, but in smaller herbaria the position may require only a master's degree. Degrees required are related to some branch of botany, most commonly plant systematics.

The curator oversees the selection of **specimens** to be placed in the collection. Specimens are selected for their quality and completeness. The curator knows the contents of the general collection in the herbarium, and selects specimens that add new information. She/he also chooses specimens that are used in specific studies, called voucher specimens.

specimen object or organism under consideration

Those who process new specimens are trained by the curator to mount the collections on herbarium paper, to prepare them for accession into the herbarium, and to file the specimens. Sheets must be carefully mounted with a label that contains the collector's information, and then a number (called an accession number) is stamped on each sheet. The plant is sterilized and filed. The filing must be done carefully, as a misfiled plant may not be seen again for years until it is accidentally found. At university herbaria, student workers are hired to assist in all of the herbarium functions, and that is how many interested people get their introduction to an herbarium and get their first botanical job experience.

Often the information on an herbarium sheet is entered into a computer database. This information is kept in the herbarium for visitors and users, and increasingly such information is being posted on Web sites. Searchable databases may subsequently be linked with similar databases from other herbaria and accessed by any computer.

Visitors and users of the herbarium may include the public, researchers, students, or representatives from public agencies trying to solve problems or accurately enforce laws and regulations. The curator is both a botanist and public servant who has knowledge of the local plants. He/she must try to confidently identify specimens brought to the herbarium, including those that are not in ideal condition. Accurate identification is a skill that takes time to develop. The curator is knowledgeable about the literature available, reads new articles as they are published, and acts as a librarian who is able to direct people to the resources they need to find answers to their questions.

Herbaria both borrow and lend specimens so that researchers working at specific herbaria can study them. The borrowed specimens are treated carefully, kept in herbarium cabinets, and before the sheet is returned a small label (called an annotation label) is attached describing the study or naming the specimen. Herbaria also exchange duplicates of specimens so that other facilities can have more complete collections.

Herbarium curators usually have their own research projects. Often the curator becomes a specialist and publishes papers on her/his research. Publications from an herbarium inform the rest of the botanical world that the herbarium is active and is the location of expertise. The curator is also an administrator, determining the needs of the herbarium and budgeting money to effectively accomplish the herbarium's mission. The scope of this responsibility is varied from herbarium to herbarium. Herbaria may be associated with universities or museums, publicly or privately funded, or a combination of both. Many changes are coming to herbaria as science finds new information and paths of research. An herbarium curator is at the center of many and varied disciplines, protector of a historical asset, and a growing resource. Curators of herbaria are generally dedicated people who are fascinated by their jobs. SEE ALSO Taxonomist.

Philip D. Jenkins

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Cyanobacteria

Cyanobacteria are a **morphologically** diverse group of photosynthetic prokaryotic microorganisms that form a closely related **phylogenetic lineage** of eubacteria. Historically, cyanobacteria were classified with plants and called blue-green algae, although true algae are **eukaryotic**. Cyanobacteria appear early in the fossil record with some examples approximately 3.5 billion years old. Stromatolites are large, often fossilized colonies of cyanobacteria that build up layer upon layer. Cyanobacteria contributed to the conversion of Earth's atmosphere from an **anoxic**-reducing environment to one rich in oxygen. Commonly studied genera include *Anabaena*, *Lyngbya*, *Microcystis*, *Nostoc*, *Oscillatoria*, *Synechococcus*, and *Synechocystis.*

morphological related to shape

phylogenetic related to phylogeny, the evolutionary development of a species

lineage ancestry; the line of evolutionary descent of an organism

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

anoxic without oxygen

Marine and freshwater aquatic environments (including aquaria) are rich in cyanobacteria, either free-living, in biofilms, or in mats. Cyanobacterial species (*Microcystis* or *Oscillatoria*) that produce compounds (e.g., microcystins) toxic to humans and animals are sometimes associated with large-scale blooms in aquatic systems. Curling crusts on soils are often due to cyanobacteria. Pioneer communities on bare rock surfaces often include cyanobacteria or lichens, the latter existing as symbiotic associations of cyanobacteria and fungi. Cyanobacteria are found in extreme environments, including hot springs, desert sands, hypersaline ponds, and within the rocks of dry Antarctic valleys. Urban cyanobacteria are found as biofilms on concrete, brick buildings, and wooden fences.

Cyanobacteria are morphologically diverse, including unicellular and **filamentous** forms (branched and unbranched). Some filamentous species produce specialized cells including heterocysts, trichomes, hormogonia, and akinetes. As **prokaryotes**, cyanobacteria lack a nucleus and membrane-bound **organelles**. Photosynthetic thylakoid membranes and polyhedral bodies (carboxysomes) are visible using an electron microscope. Cyanobacteria may contain gas vacuoles, polyphosphate granules, and inclusions of cyanophycin, a nitrogen storage **polymer**.

filamentous thin and long

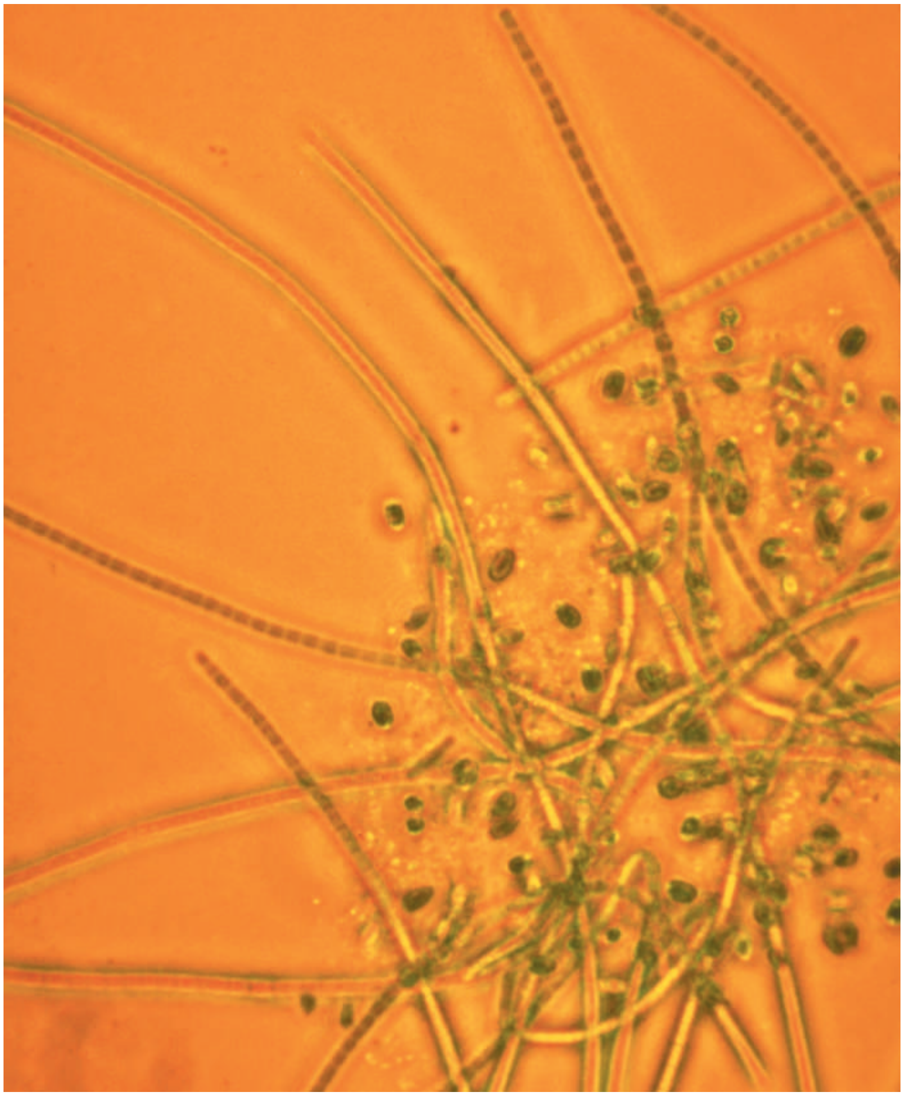
prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

organelle a membrane-bound structure within a cell

polymer a large molecule made from many similar parts

A distinguishing feature of cyanobacteria is their photosynthetic pigment content. In addition to chlorophyll *a*, cyanobacterial thylakoids include phycobilin-protein complexes (phycobilisomes) containing mixtures of phycocyanin, phycoerythrin, and allophycocyanin, which give cyanobacteria their characteristic blue-green coloration. Phycobilisomes harvest light at wavelengths (500 to 650 **nanometers**) not absorbed by chlorophylls. Most

nanometer one-millionth of a meter



Anabaena, a genera of cyanobacteria, greatly improve crop yields when cultured in the soil of rice paddies.

cyanobacteria perform oxygenic photosynthesis like higher plants. A few species perform anoxygenic photosynthesis, removing electrons from hydrogen sulfide (H_2S) instead of water (H_2O). There is a general dependence on carbon dioxide as a carbon source, although some cyanobacteria can live **heterotrophically** by absorbing organic molecules. The reductive pentose phosphate pathway predominates for carbon assimilation, as cyanobacteria have an incomplete tricarboxylic acid (Krebs) cycle.

heterotroph an organism that derives its energy from consuming other organisms or their body parts

enzyme a protein that controls a reaction in a cell

Many species of cyanobacteria fix atmospheric dinitrogen (N_2) into ammonia (NH_3) using nitrogenase, an **enzyme** that is particularly sensitive to the presence of oxygen. In filamentous cyanobacteria, such as *Anabaena* and *Nostoc*, certain cells differentiate into heterocysts (thick-walled cells that do not photosynthesize), in which nitrogen fixation occurs under reduced oxygen concentrations. Cyanobacterial nitrogen fixation produces bioavailable nitrogen compounds that are important in nitrogen-limited aquatic ecosystems and plays an important role in global nitrogen cycling.

No other group of microbes participates in as many symbioses as cyanobacteria, including extra- or intracellular relationships with plants,

progenitor parent or ancestor

chloroplast the photosynthetic organelle of plants and algae

fungi, and animals. This phenomenon, coupled with the plantlike photosynthesis of cyanobacteria, suggests that cyanobacteria were the **progenitors** of **chloroplasts**. Endosymbiotic theory holds that ancestral eukaryotic cells engulfed the ancient cyanobacteria that evolved into modern plastids. Better candidates may be prochlorophytes, oxygenic photosynthetic bacteria that contain chlorophyll *a* and *b* and form an evolutionarily related group with cyanobacteria and plastids. SEE ALSO AQUATIC ECOSYSTEMS; ENDOSYMBIOSIS; EUBACTERIA; NITROGEN FIXATION; PHOTOSYNTHESIS, CARBON FIXATION AND; PHOTOSYNTHESIS, LIGHT REACTIONS AND; WETLANDS.

Mark A. Schneegurt

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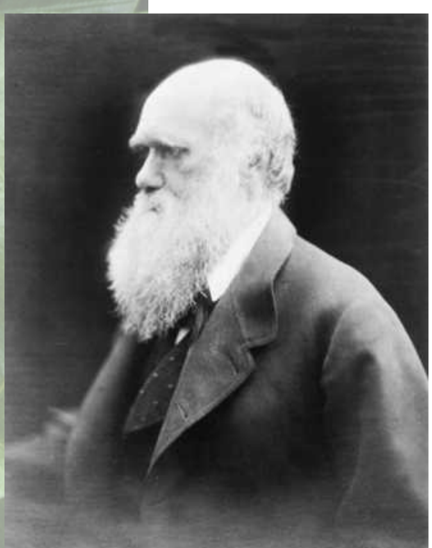
Cytokinins

See Hormones.

D

Darwin, Charles

English Naturalist
1809–1882



Charles Darwin.

Charles Darwin was probably the most influential scientist of the nineteenth century. He is best known for his revolutionary ideas that species transmute, or evolve, by means of the primary mechanism of natural selection, ideas he set forth in his great work *On the Origin of Species* in 1859. This work shaped intellectual, political, and philosophical attitudes of the nineteenth century and fundamentally transformed humanity's understanding of its origins in terms of natural rather than supernatural causes. Though deemed controversial, his ideas continued to hold sway through the twentieth century. For these reasons, he is generally regarded as not only one of the great figures of the history of science, but also one of the great figures of the western intellectual tradition.

Early Life and Background

transmutation change from one form to another

Charles Robert Darwin was born on February 12, 1809, in Shrewsbury, England, into a wealthy, distinguished family. His paternal grandfather was Erasmus Darwin, a physician who delved into many subjects, including poetry, and who made one of the early statements in support of **transmutation**, or the belief that species are changeable and not fixed. His father was Robert Waring Darwin, an equally successful physician, who practiced in Shrewsbury. His mother was Susannah Wedgwood, the daughter of the industrialist potter Josiah Wedgwood.

Charles Darwin's education began at home, largely through the efforts of his older sisters who took the place of his mother when she died prematurely. He was eventually sent to a local day school, and in 1818 he entered

Shrewsbury School, one of the great English public schools of the nineteenth century. Though a poor student, Darwin developed a keen interest in natural history at a young age, and spent many of his leisure hours collecting insects and plants.

In 1825 Darwin enrolled at Edinburgh University with the intent of studying medicine. He was unsuccessful in his formal studies and developed a distaste for surgery. Two years later, he gave up his medical aspirations and left Edinburgh for Cambridge University, where he intended to study theology in the hopes that he could lead the respectable life of a country vicar. He failed to perform adequately in his formal studies, however. His one true interest remained in natural history, an interest that was encouraged by the professor of botany at Cambridge, John Stevens Henslow (1796–1861). Darwin became so enamored of this mentor that he came to be known as "the man who walks with Henslow." Another important influence on Darwin at this time was the professor of geology, Adam Sedgwick (1785–1873). Though Sedgwick provided the only formal training in science that Darwin was to receive, it was Henslow who provided directive influence in Darwin's life after he recommended him to the Admiralty, which was preparing a survey expedition to chart the coastline of South America. Darwin was to serve as companion to the captain, Robert FitzRoy, on the H.M.S. *Beagle.* On occasion he was to serve as ship's naturalist. The five-year voyage of the *Beagle*, beginning on December 31, 1831, and ending on October 2, 1836, was to prove the pivotal experience in shaping Darwin's subsequent scientific work. Darwin returned to England much altered from his experiences. He had not only matured during the voyage, but also distinguished himself with his superb collections, so much so that he became the center of attention in scientific circles.

Scientific Work, 1831–59

While aboard the H.M.S. *Beagle*, Darwin was struck by the diversity of life that he encountered and how beautifully adapted it was to diverse environments. As he traveled up and down the eastern coastline of South America he was especially interested in the geographic distribution of plants and animals that appeared to replace each other. More importantly, he was taken by the fact that extinct fossils in the area closely resembled living forms of related species, and that the flora and fauna on oceanic islands bore a striking similarity to the nearest continental landmass. He became particularly interested in the distribution of the flora and fauna of a string of recently formed volcanic islands known as the Galapagos, after the unique species of tortoises that are found there. Darwin noticed that each island in the group had an entirely unique flora and fauna. He also noticed that the species bore a striking resemblance to the species on the nearest continental landmass, the western part of South America. With insights from British geologist Sir Charles Lyell (1797–1875), who espoused a **uniformitarian** rather than a **catastrophist** geological theory, the weight of this geographic evidence suggested to Darwin that species had not been independently created. They had instead slowly diverged from preexisting species as they came to **colonize** new habitats and as they adapted to new ecological **niches**.

uniformitarian the geologic doctrine that formative processes on Earth have proceeded at the same rate through time since Earth's beginning

catastrophism the geologic doctrine that sudden, violent changes mark the geologic history of Earth

colonize to inhabit a new area

niche the role of an organism in its habitat, involving the whole variety and ecological relationships of which it is a part

Although Darwin had recognized this geographic pattern, he did not have an explanation or a mechanism for how the flora and fauna were able to adapt themselves to their respective environments. The mechanism of evolution occurred to him only after his return to England and after he had been able to sort through his collections. The decisive moment came two years after his return while he was reading English economist Thomas Malthus's *An Essay on the Principle of Population* (1798). In this famous essay, Malthus had noticed that human populations, if left unchecked, had the tendency to double each generation. In other words, their pattern of growth was exponential. But Malthus also noted that resources necessary to sustain populations increased at a much slower rate, or arithmetically. To Malthus, this meant one thing: that at some point members of the population were subjected to strong competition for those resources, and that such events as war, disease, and famine were natural ways to keep the population in step with available resources. Darwin realized that this principle could just as easily apply to populations of animals and plants. In the competitive struggle for existence, Darwin added, those individuals who bore favorable characteristics would be more likely to survive to reproduce. They in turn were more likely to transmit these favorable characteristics to their offspring. Given enough time, subsequent generations of their offspring would depart from the parental types. Given more time, Darwin added, they would diverge even further from their ancestral types, eventually leading to new species. This principle of divergence strengthened and supported what Darwin called his theory of descent with modification by the mechanism of natural selection. It is what accounted for the origin of species.

Although he had formulated his theory between 1837 and 1838—now recognized as the critical period for Darwin's intellectual development—Darwin did not set these ideas formally on paper until 1842 in a rough sketch, and in 1844 in what is called his historical essay. He showed this short manuscript only to his close friend, the young botanist Joseph Dalton Hooker (1817–1911). Instead of publishing his theory, Darwin continued his research into the late 1850s, hoping to collect enough evidence to support what he knew to be a very controversial theory. Between 1837 and 1859 Darwin therefore engaged in a number of research projects intended to lend support to his theory, including some botanical studies to understand adaptation.

After formulating his theory, Darwin's plan was to collect data carefully from workers around the world to fortify his theory. In particular he was interested in both plant and animal breeding practices, which had been created by artificial selection, a form of selection through human intervention. He became especially interested in pigeon breeding, a popular hobby for Victorians, because it clearly demonstrated the stunning range of variation possible through artificial selection.

In 1839 Darwin married his first cousin, Emma Wedgwood, and in 1842 the couple left London to settle in the nearby village of Downe. There Darwin could escape from the bustle of the city and devote himself fully to his research. The quiet country environment removed from society was also important to Darwin, who began to suffer from an unknown illness, which sometimes left him incapacitated. Only a select group of scientists had access to him. By the 1850s, the inner circle of Darwin's friends, in addition to Hooker and Lyell, included a young morphologist, Thomas Henry Huxley (1825–1895), who became Darwin's intellectual defender.

Publication of *On the Origin of Species*

Darwin's peaceful existence was shattered in 1858 when he received a letter from a young naturalist named Alfred Russel Wallace (1823–1913). Wallace had been exploring the Malay Archipelago in Southeast Asia. Darwin faced the contents of the letter with mixed feelings: Wallace had reproduced much of Darwin's secret theory, leaving Darwin to face a possible priority dispute. At the advice of the inner circle, Darwin and Wallace published their work jointly in the *Journal of the Linnaean Society* in 1858. Darwin used the push from Wallace to complete a longer account of his theory, and included evidence he had gathered not only from his own observations and experiments, but also from his correspondence with naturalists and breeders from around the world. Darwin intended this work to be merely an abstract of his longer theory, but the published book was over four hundred pages. Its full title in the first 1859 edition was *On the Origin of Species or the Preservation of Favored Races in the Struggle for Life.* The book appeared in bookstores on November 24, 1859, and promptly sold out on the first day. It was to go through six editions.

Darwin's life was permanently changed as the theory that Huxley named "evolution" became a topic of heated debate. It was criticized on the scientific front because it failed to provide an adequate theory of heredity and because blending theories of heredity, popular at the time, would have led to a dilution of favorable characteristics. This problem was addressed only after Darwin's death by the rediscovery of Gregor Mendel and his theory of heredity in 1900. Another problem was the age of Earth, which was thought to be about four hundred million years old, an insufficient amount of time to account for the slow, gradual process that Darwin envisioned. This problem was solved after the discovery of radioactivity in the late nineteenth century that, when included in calculations, increased the age of Earth to nearly five billion years, an estimate of time long enough to account for evolution. Yet another difficulty was the fact that Darwin had no direct proof for a process that took place over a long stretch of time. Darwin knew this, and predicted that it would take some fifty years to accumulate enough evidence to support this theory. This was in fact provided beginning in 1920s with the example of industrial melanism in the peppered moth, *Biston betularia*.

More difficult to resolve were the theological and philosophical questions that followed from the mechanism of natural selection. Even though Darwin had only one line on human evolution in the book, the theory implied that humans were subject to the same mechanistic process as plants and animals. Mechanistic and materialistic, natural selection also challenged the argument for God's existence from design and led to a nonpurposive view of the world. To some, like the poet Alfred, Lord Tennyson, a competitive nonpurposive view of nature implied that it was "red in tooth and claw."

Despite a storm of controversy over the mechanism, the fact of evolution was rapidly accepted by scientists. Only after the mechanism of heredity was understood and only after the science of genetics was integrated with natural history was the debate over the mechanism of natural selection extinguished. This did not take place until the interval of time between 1920 and 1950 and was part of the event called the *evolutionary synthesis.*

Botanical Work

From the start, plants figured prominently in the development of Darwin's ideas of evolution by means of natural selection. Examples from the plant world abound in *On the Origin of Species* and *Variation of Plants and Animals Under Domestication* (1868). Not only were plants easily studied and bred, but they showed a stunning assortment of adaptive features. They were to prove one of Darwin's favorite objects of study, becoming the basis of no less than seven books, most of which appeared in the latter part of Darwin's life.

Darwin's first book on plant evolution was titled *Fertilization in Orchids* (1862). He chose to study orchids because of the range of adaptations they displayed with respect to fertilization. Darwin recognized that these elaborate adaptations served to facilitate cross-pollination by insects such as bees. For this reason, cross-pollinated plants had flowers with bright colors and fragrant nectaries to attract bees and other insects, while wind-pollinated plants, which did not have to attract insect pollinators, had flowers with little or no color.

Darwin also observed that plants that seemed to have one or few flowers had the tendency to be hermaphrodites, having flowers of both sexes on the same plant. Bigger trees with a large number of small flowers, however, usually had flowers of only one sex. To Darwin, this implied that flowers had adapted mechanisms to ensure cross-pollination. This likely increased the variability, and also increased the vigor of the offspring. Darwin performed numerous experiments to understand the manner in which cross-pollination took place in plants and to understand the adaptive function of increased variability. In the process he noted the phenomenon of heterosis, or **hybrid** vigor, in the progeny of cross-pollinated plants. He also began to unravel the adaptive functions of sexual reproduction.

hybrid a mix of two species

Darwin's work in pollination mechanisms appeared in two books. The first was *Effects of Cross and Self Fertilization* (1876), which was followed by *Different Forms of Flowers on Plants of the Same Species* (1877).

twining twisting around while climbing

Darwin was also interested in the adaptive functions of climbing plants. He found that the phenomenon of **twining**, or the differential bending of plants in a clockwise or counterclockwise manner around an object, permitted young or weak plants to raise themselves higher up off the ground. This maximized exposure to air and sunlight in a relatively short time, and without the costly and time-consuming investment of woody supportive structures. The various means used by plants to climb were explored in his book *Climbing Plants* (1875). The mechanisms by which this and other plant movements took place was explored in *Power of Movement in Plants* (1880). In this book Darwin explored plant tropisms, or the manner in which plants were able to grow toward light. He determined that the stem bends toward the light because of differential growth rates: the illuminated side grew more slowly than the unilluminated side so that shoot tips appeared to bend toward the light. He postulated the existence of a substance that was diffused from the apex downward that affected growth rates. These investigations anticipated the existence and action of plant hormones.

Darwin then directed his attention to other types of movements in plants, including mechanisms for prey capture in insectivorous plants such as the sundew, *Drosera rotundifolia* (1880). After detailed observation and experimentation, Darwin concluded that carnivorous plants had acquired the ability to live in nitrogen-poor soil with little or no root structure by feeding on prey. In addition to developing sensory apparatus to detect and capture prey, plants had also developed a digestive system capable of breaking down proteins. Most of these observations, including experiments with the sundew plants, were the focus of his book *Insectivorous Plants* (1875).

Darwin's last book relating to plants was a work with a strangely ecological theme: the action of worms in turning up soil. After experiments that ran for more than fifty years, Darwin postulated that earthworms played a vital ecological role: they fed on dead leaves and other organic matter and excreted this back into the soil. In so doing, earthworms served to aerate the soil and recycle vital nutrients. These results, including quantitative estimates of how much soil was processed by earthworms, were included in *The Formation of Vegetable Mould Through the Action of Worms* (1881).

Darwin's botanical work is notable for its detailed observations and simple, elegant experiments. These were performed in the confines of Darwin's backyard or at greenhouses at his home in Downe. Despite the fact that some of these are now classic experiments reproduced by students the world over, they were judged harshly by the leading German plant physiologist of the late nineteenth century, Julius von Sachs (1832–1897). A revolutionary experimentalist who introduced powerful analytical laboratory methods to botanical science, launching the "New Botany," Sachs thought Darwin's naturalist tendency and simple backyard experiments to be antiquated and amateur. Nonetheless, Darwin's botanical work remains the cornerstone of his studies on variation and mechanisms of adaptation in plants and is significant for his keen insights.

The book on earthworms was published just six months before Darwin's death. Until his end, Darwin remained a productive scientist. Some of his most imaginative work was performed toward the end of his long life. His was a happy and productive life in a home filled with the voices of his ten children and numerous grandchildren. On his death in 1882, he received a rare honor for a scientist: he was given a state burial and was buried at Westminster Abbey. SEE ALSO CARNIVOROUS PLANTS; COMPOST; EVOLUTION OF PLANTS; EVOLUTION OF PLANTS, HISTORY OF; HOOKER, JOSEPH DALTON; MENDEL, GREGOR; ORCHIDACEAE; PHYLOGENY; SACHS, JULIUS VON; TROPISMS AND NASTIC MOVEMENTS.

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Deciduous Forests

angiosperm a flowering plant

The temperate deciduous broadleaf forest (TDBF) is composed of broadleaf **angiosperm** trees like the oaks, maples, and beeches familiar to many Americans and Europeans. The forests exist best in moderate climates that are neither too hot nor too cold and neither too wet nor too dry. In addition to the temperate zone, deciduous forests are found in tropical and subtropical climates in open savannas and/or in closed forests. While there are roughly thirty families and sixty-five genera in the TDBF, variation in the precise definition and defined area of the forest make absolute numbers impossible. With thousands of species, the TDBF is a highly diverse biome.

North American Temperate Deciduous Broadleaf Forest

Worldwide, there are five major groups of TDBFs. Within each group, botanists define TDBFs by the species that tend to occur in a given area. These collections of species, together with their environment, are called associations. Eastern North America today contains the most extensive TDBF. The forest reaches from about longitude 95°W (just west of the Mississippi River) to the Atlantic coast and from 30 to 45°N, thereby forming a quadrant that includes most of the northeastern quarter of the United States. The eastern United States TDBF was almost completely deforested for agricultural purposes by 1850. At that time, land was opened for agriculture in the Mississippi valley, and many farms were abandoned. Pines grew well in the remaining grassy fields, but after a catastrophic hurricane in 1937, the TDBF grew back. Today, there is much more TDBF in the United States than there was one hundred years ago (though still less than before the arrival of European settlers).

There are nine generally recognized associations in the United States TDBF, each defined by differences in vegetation (see accompanying table). Though the species are representative of common dominants, many other species exist. TDBF associations are not completely separate. Many species, such as northern red oak and sugar maple, exist in more than one association. Nor are the boundaries between the associations sharp and easily identifiable. In particular, the Western Mesophytic association can be difficult to distinguish from its neighbors to the east (Mixed Mesophytic) and west (Oak-Hickory). Associations can change with time too. The Oak-Chestnut association is now almost completely devoid of chestnut, but many people still use the association name even though it is now mostly oak and maple. Association names in North America and elsewhere are most useful for distinguishing broad differences in forest type often associated with variation in soils, topography, and climate.

European, Asian, and South American Temperate Deciduous Broadleaf Forest

The European TDBF, stretching through most of Europe (except for very hot and cold areas) from the Atlantic Ocean to the Ural Mountains, is

TEMPERATE DECIDUOUS BROADLEAF FOREST (TDBF) ASSOCIATIONS IN THE UNITED STATES

Type of Association	Location	Common Species
Mixed Mesophytic	Unglaciated central Appalachian Mountains	White basswood (*Tilia heterophylla*), Carolina basswood (*Tilia caroliniana*), American basswood (*Tilia americana*), sugar maple (*Acer saccharum*), black maple (*Acer nigrum*), yellow buckeye (*Aesculus octandra*), northern red oak (*Quercus rubra*), white oak (*Quercus alba*), and eastern hemlock (*Tsuga canadensis*); transitional forest between Mixed Mesophytic and Oak–Hickory
Western Mesophytic	West of the southern Appalachian Mountains	White oak, yellow buckeye, white basswood, American beech (*Fagus grandifolia*), and sugar maple; dominant species highly variable
Oak–Hickory	Western boundary of the central and southern TDBF (western Missouri and Arkansas)	White oak, red oak (*Quercus borealis maxima*), black oak (*Quercus velutina*), bitternut hickory (*Carya cordiformis*), and shagbark hickory (*Carya ovata*); drought stress to the west is leading to increased grass cover and the eventual elimination of the TDBF in the Great Plains
Oak–Chestnut	Eastern Appalachian Mountains	Chestnut oak (*Quercus prinus*), northern red oak, and red maple (*Acer rubrum*); before 1904 this association was dominated by *Castanea dentata* (chestnut), but between 1904 and 1950 the chestnut blight killed virtually all mature chestnuts. *Castanea* was replaced by oaks, but the Oak–Chestnut association name is still used
Oak–Hickory–Pine	Piedmont region, southeastern Appalachian Mountains, mid-Atlantic states	Those in Oak-Hickory association with the addition of loblolly pine (*Pinus taeda*), shortleaf pine (*Pinus echinata*), Virginia pine (*Pinus virginiana*), longleaf pine (*Pinus palustris*), and Caribbean pine, also called slash pine and Jersey pine (*Pinus caribaea*); association similar to Oak–Hickory, and plantation forestry with coniferous species widely practiced
Southeastern Evergreen	Southern boundary of the TDBF (southern Arkansas through central Georgia)	Longleaf pine, slash pine (*Pinus elliottii*), loblolly pine, and shortleaf pine; transition between angiosperm and gymnosperm forest. Large oak stands exist, as well as limited areas of evergreen broadleaf trees (such as magnolia). Coniferous species dominate
Beech–Maple	South of the central Great Lakes	American beech, sugar maple, American elm (*Ulmus americana*), black walnut (*Juglans nigra*), white ash (*Fraxinus americana*)
Maple–Basswood	West of Lake Michigan	Sugar maple, American basswood, northern red oak, slippery elm (*Ulmus rubra*), American elm, and bitternut hickory; smallest association
Hemlock–White Pine–Northern Hardwood	Northern boundary of the TDBF (Canada and New England from the northern Great Lakes to Nova Scotia)	Sugar maple, American beech, yellow birch (*Betula alleghaniensis*), American basswood, red maple, aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), eastern white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), larch (*Larix lacricinia*), and northern white cedar (*Thuja occidentalis* and *Thuja canadensis*); largest association

the second-largest TDBF. Due to the moderating influences of the Gulf Stream, the TDBF exists as far as 60°N in northwestern Europe. Forests in Europe have been extensively modified by humans for more than two thousand years and are some of the most manipulated forests in the world. In the northern European TDBF, birch species are common, while in the middle European latitudes, beech (*Fagus sylvatica*) is widely distributed and commercially valuable. Towards the south, various oak and maple species abound. As in North America, much of the once-cleared TDBF is now regrowing. The European TDBF is replaced by drought-resistant shrubs and evergreen broadleaf trees in the south and the boreal coniferous forest in the north.

The last three TDBF areas are much smaller than the first two. East Asia, from 30° to 60°N and from central Japan to longitude 125°E in the northwest and longitude 115°E in the southwest, originally maintained very large forests. Today, even though the species mix is still very diverse, much of the East Asian forest outside of Japan is currently under **cultivation** and most existing forest fragments are protected refuges or in areas unsuitable for agriculture. Nearly all TDBF genera are present in East

cultivation growth of crop plants, or turning the soil for this purpose

Leaves of the sugar maple (*Acer saccharum*) provide rich hues of red during the autumn while birch and oak display brilliant orange and yellows.

Asia, especially China. The Near East between 35° and 45°N, including areas around the eastern Black Sea and mountainous regions in Iran and near the Caspian Sea, supports a diverse TDBF. Finally, a narrow strip of South America including southern Chile and Argentina contain TDBF. *Acacia caven* and seven *Nothofagus* species are also found there. In nearly all cases, the deciduous trees of South America occur in mixtures with evergreen broadleaf species.

Of the three major TDBFs, East Asia has by far the greatest diversity, followed by North America and Europe. East Asia was glaciated less severely than America and Europe, so most species were able to survive with little difficulty. In North America, the north-to-south orientation of major mountain ranges allowed species to migrate, and species diversity here is only slightly lower than in East Asia. In Europe, on the other hand, the east-to-west mountains caused the TDBF to be trapped by advancing glaciers. Many modern European TDBF species survived only in the Near East TDBF and migrated back after the glaciers retreated. Consequently, Europe has very low-species diversity.

Climate and Soils

TDBFs are generally restricted to a warm temperate climate with four identifiable seasons in which the average temperature of the coldest month is between 3 and 18°C and the average temperature of the warmest month exceeds 10°C. The length of the frost-free period ranges from 120 to over

250 days. **Precipitation** is year-round and averages between 80 and 200 centimeters per year. Snowfall can range from nonexistent in the southeastern United States to extremely heavy in northern habitats. Climates that are wet and warm all year are occupied by tropical forest consisting of broadleaf evergreen trees. As climates become drier, as occurs at the western edge of the Oak-Hickory association, drought stresses are too extreme for TDBF and grasses become dominant. To the north of the major TDBF, extreme cold, short growing seasons and poor soils favor evergreen coniferous forests. TDBF soils tend to be deep and fertile and, unlike some soils in the northern coniferous forest, do not freeze year-round. For this reason, TDBFs have historically been popular for agricultural use.

precipitation rainfall

Leaves and Phenology

Deciduous leaves are the most distinctive feature of the TDBF. In the fall, spectacular reds, oranges, and yellows produce breathtaking displays across the TDBF. Why does this occur? During autumn, as temperatures cool and days shorten, trees send hormonal signals to their leaves causing them to turn colors and fall off the branch. First, leaves form a barrier between the leaf and the branch, known as the **abscission** layer. At the same time, chlorophyll, the compound that gathers light for photosynthesis, begins to degrade in the leaf. Many of the nutrients in the leaf are sucked back into the tree for next year's leaves. Chlorophyll is responsible for the usual green leaf color: once it is gone, yellow and orange pigments that were there all along become visible. Some of the sugar in the leaves of oaks and maples may be converted into red colors. Once the leaf is totally shut down and no longer conducting any photosynthesis, the abscission layer becomes very brittle. Any small breeze can snap the leaf off at this point. In the spring, using carbon from special storage cells in the trunk, trees grow a new batch of leaves. In an evolutionary adaptation designed to maximize the amount of light received, shrubs and small trees growing in the understory will begin growth before the overstory.

abscission dropping off or separation

The study of any recurring biological cycle and its connection to climate is called phenology. Patterns of bird migration and insect outbreaks are examples of phenological cycles. For centuries, scientists have been studying phenology in the TDBF. In the deciduous forest, phenology refers to the timing of spring leaf growth and fall leaf drop and their relationship to climatic variation. Observational evidence has shown that TDBF phenology is highly sensitive to variation in weather. Warm springs will cause leaves to grow earlier, sometimes by up to as much as one month. Conversely, plants respond to a cold fall by dropping their leaves earlier. Phenological cycles in the forest are one possible indication that plants are responding to global warming. If temperatures are warming, the growing season should be getting longer. Most evidence between 1950 and 2000 suggests that the duration of the growing season has lengthened by several days in many forests. TDBF leaves are not only beautiful, they can also provide very useful scientific observations.

Plant-Animal Interactions

The TDBF supports rich plant-animal interactions in all three of the classic ecological relationships between two species or organisms: mutualism, commensalism, and antagonism.

Mutualism. In a mutualistic relationship, both participants receive a benefit. Mutualisms are quite a bit like bargains or trades. In flowering plants, most pollination does not take place with wind. Pollen grains must be physically transported from the male stamen to the female stigma where the process of fertilization begins. In the past, angiosperms relied on the chance event that an insect would happen to brush against the stamen on one flower and then on the stigma of another flower. This was very inefficient and plants eventually evolved in such a way as to greatly increase the chances of successful pollination. While a few TDBF trees are wind-pollinated, most use nectar, a sweet sugary substance, to lure pollinators. While they eat the nectar, pollinators brush the stamen and collect pollen. When they visit a female flower, the pollinator brushes the stigma, transporting the pollen and beginning fertilization. Brightly colored flowers and vivid aromas also attract pollinators, as do ultraviolet markings on some flowers. In the TDBF, insects (especially bees) are the most important pollinators. Other pollinators in the TDBF include moths, butterflies, wasps, flies, and birds.

Commensalism. In a commensal relationship, one participant gains a benefit without harming the other. As in many forests, small mammals such as raccoons, squirrels, and mice as well as such birds as owls use trees for habitat in a commensal relationship. Some insects have evolved to look almost exactly like twigs or leaves. This makes it difficult for predators to locate them in the trees.

Antagonism. Organisms in an antagonistic relationship benefit at the expense of the other organism. Antagonistic relationships are common. Herbivory by insects, in particular the gypsy moth, can cause extensive damage to the TDBF. White-tailed deer and other ungulates eat leaves and can be the most destructive animals in the forest. In a response to browsing pressures, some trees have evolved leaves with distasteful **toxins**. The black-tailed deer, though, has developed special chemicals in its saliva to neutralize these toxins. In the future, it is likely that trees will evolve new defensive toxins. This process of back-and-forth evolution between **herbivores** and plants is an example of a process called coevolution.

toxin a poisonous substance

herbivore an organism that feeds on plant parts

Threats to the Temperate Deciduous Broadleaf Forest

Farming has historically represented the greatest threat to the TDBF. Today's TDBF has extensively regrown in the eastern United States, but in Europe and East Asia, the other two major areas, the forest is still highly fragmented. Species diversity fortunately tends to remain high even in highly scattered groups. Future regrowth can occur rapidly from these isolated or protected areas.

Fungal diseases are currently much more serious threats. Plants all over the world have fungal pests to which they are usually well adapted. Serious problems arise when these diseases are transported to forests that have no defenses. The chestnut blight, introduced to America from Europe in 1904, is the best-known example. In four decades, the chestnut blight eliminated a popular and valuable tree from an entire continent. Dutch elm disease reached the United States by 1930 and to date has killed millions of elms. Humans are almost always the cause of these introduced diseases. Fungi can easily store themselves on ships, cars, or trains. As global commerce increases, it is likely that humans will continue to accidentally introduce diseases into the TDBF. SEE ALSO BIOME; CHESTNUT BLIGHT; COEVOLUTION; CONIFEROUS FORESTS; DECIDUOUS PLANTS; DUTCH ELM DISEASE; FORESTER; FORESTRY; TREES.

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Deciduous Plants

A perennial plant that seasonally loses its leaves (and/or stems) is deciduous. This loss is typically related to water stress; for example, green portions of the plant are shed during the dry season. Dry does not have to mean no (or low) **precipitation**. It simply means that little water is available for the plant. Winter in some areas brings heavy snows; unfortunately, the ground water is frozen and unavailable for the plant. Most of the water lost by a plant occurs because of transpiration (evaporation through its leaves). By dropping its leaves during the dry season, deciduous plants are able to avoid dehydration.

precipitation rainfall

In colder climates, it is typically the reduction in both day length and temperature that cause the process to begin. In desert (or equatorial) regions, the winter (shortest days) is often the rainy season. Many plants in these areas do not develop leaves or aboveground portions until they have sufficient moisture. Loss of these portions is more closely associated with a decrease in moisture rather than a change in day length.

Whether caused by shorter day length, cooler temperatures, or decreased moisture availability, the process is the same. Environmental cues prompt the production of an important hormone, ethylene, which in turn induces the formation of an abscission zone. This zone is near the point of attachment of leaf (or stem) to the rest of the plant. The **abscission** zone is composed of two parts: the separation layer and the protection layer. The separation layer marks the area where the leaf will break away from the plant

abscission dropping off or separation

An oak tree in wintertime in the Shenandoah National Park in Virginia.

or abscise. The protection layer seals the wound left by the dropped leaf, protecting the plant from infection and moisture loss.

The formation of the abscission zone breaks many of the connections the leaf had with the plant. This causes a decrease in the amount of water available to the leaf, causing a consequent decrease in chlorophyll production. With the loss of chlorophyll, the other pigments in the leaf (anthocyanins and carotenoids) show through. The net result is the dramatic fall color changes seen in many deciduous forests.

Not all perennial plants are deciduous. Many are considered evergreen, since they retain their leaves throughout the year. Deciduous and evergreen plants can often be found in the exact same habitats growing next to one another. Each has its own adaptations to deal with seasonal water stress. For instance, some adaptations that evergreens have to deal with dry conditions include thick, waxy leaves, leaves with low surface area (conifer needles, for example), or water storage tissues (such as cacti).

There is a cost to dropping leaves, which is why some perennial plants are not deciduous. It can take a lot of nutrients from the soil to produce the number of leaves produced in an average growing season. In areas where nutrients are plentiful, an annual leaf drop is not a problem. However, in areas with nutrient poor soils, dropping leaves may be very costly for the plant. The advantages of decreased water stress and the detriments of a seasonal loss of nutrients must be balanced to insure an evolutionarily stable strategy. SEE ALSO Anthocyanins; Carotenoids; Chlorophyll; Deciduous Forests; Hormones; Leaves; Pigments; Trees.

Steve Dickie

Decomposers

Decomposers are the choppers, shredders, plowers, and dissolvers of the biological world. They break down tree leaves, dead flowers, grass blades, old logs in forests, and plant roots into small parts, and, finally, into carbon dioxide, water, and numerous basic chemical compounds in soils, water bodies, and sediments. Organisms involved in decomposition vary from earthworms that drag leaves into their burrows, chew up parts of the leaves, and pass them through their guts to microscopic bacteria that make the final breakdown of fragments into basic chemicals. Some decomposers are specialized and act most effectively on only, for example, oak leaves or maple seeds. Others decompose parts of many plant or animal remains that fall on the soil or into a stream or lake. Most decomposers are often not visible, but in some lawn areas, especially under deciduous trees, we can see little volcano-like earthworm mounds. Mushrooms in our gardens and forests are the visible parts of fungi that are decomposing plant and animal remains in the soil.

Decomposers are the ultimate recyclers of land and water **ecosystems**. As byproducts of their actions in breaking down organic matter, decomposers obtain (and release) nutrients and energy-yielding compounds. And decomposers leave behind simpler fragments for other decomposers along with simple forms of nitrogen, phosphorus, calcium, and other plant nutrients. Plant roots then can take up these nutrients to sustain new plant growth, and insects and other animals can eat the plants. So, the cycles continue. These cycles from plant organic matter, sometimes to animal tissues, then to decomposers and basic chemical compounds are essential to maintaining the world's ecosystems. Some of the residues of decomposition, and some byproducts of decomposer processes, serve to glue together mineral soil particles. This gives soils the **porosity** that allows roots to grow and water and air to enter and leave soils. These cycles maintain soil fertility in grasslands, forests, lakes, and agricultural lands.

ecosystem an ecological community together with its environment

porosity openness

Many decomposers are partners in interesting biological systems. Microscopic bacteria in the rumens—"first stomachs"—of cows decompose grass that cows eat and pass on more easily digestible substances to the real stomachs. Other bacteria in the gut "tubes" of earthworms partially decompose plant fragments, making elements and compounds available to the worms and yield nutrient-rich residues that are passed back into the soil. Some mushroom parts of wood-decomposing fungi are important foods for some insects and forest animals, including deer and small rodents. In some cases insects or animals then carry fungal parts or

Bacteria in earthworms' digestive tracts partially decompose plant fragments, yielding nutrient-rich residues that are passed back into the soil.

spores to other spots where they form new fungal decomposing systems. Many small insects and other arthropods are important first-stage shredders and partial decomposers of plant remains. In soils where such decomposers are excluded by intensive **cultivation** or excess chemicals, the natural recycling of organic matter is slowed down. This can lead to decreased soil fertility and plant growth; farmers or gardeners are then forced to add fertilizers or mulches. Good ecosystem stewardship includes keeping active populations of decomposers of all sizes to keep the systems productive. SEE ALSO BIOGEOCHEMICAL CYCLES; CARBON CYCLE; COMPOST; FUNGI.

James R. Boyle

cultivation growth of crop plants, or turning the soil for this purpose

Defenses, Chemical

All plants produce a diverse group of chemicals whose main function is to protect the plant against **herbivores** and diseases; these are the plant's chemical defenses. Many of these compounds seem to have no role in such core plant functions as growth and reproduction, and they are synthesized in unique pathways in the plant. As a result, they are often called secondary compounds or secondary metabolites. Others, including many **enzymes**, also have functions in growth, reproduction, and acquiring light or nutrients. Even though humans have exploited these plant products for thousands of years, it was not until the 1950s that scientists reasoned that these chemicals might be produced as defenses. While many plants have physical defenses such as thorns or spines, and some are just too tough to chew, those traits block feeding by large animals only, and do nothing against diseases. Chemical defenses are potentially effective against all of a plant's enemies. The study of how plants make, deploy, and benefit from chemical defenses is an important branch of chemical ecology.

herbivore an organism that feeds on plant parts

enzyme a protein that controls a reaction in a cell

Types of Chemical Defenses

Defensive chemicals are grouped into classes based on their structures and how the plant makes them. Some classes are very large and occur in all plants, while others are smaller and may occur in only one or two plant families or a few species.

It has been estimated that, overall, plants synthesize several hundreds of thousands of different secondary compounds. New ones are reported every day. Five groups are most common, diverse, or widespread: the alkaloids, cyanogenic glycosides, terpenoids, phenolics, and glucosinolates.

Alkaloids. There are more than ten thousand different alkaloids and relatives known from plants. Alkaloids are cyclic nitrogen-containing compounds. They are widely distributed among many higher plant families, where they are often produced in roots. Their activity in animals is diverse, but many interfere with **neurotransmitters**. When consumed, many alkaloids are **addictive**. Examples include caffeine (coffee), morphine (poppy), tomatine (tomato), nicotine (tobacco), and lupine alkaloids (**legumes**).

neurotransmitter chemical that passes messages between nerve cells

addictive capable of causing addiction or chemical dependence

legumes beans and other members of the Fabaceae family

cyanogenic giving rise to cyanide

Cyanogenic Glycosides. **Cyanogenic** glycosides also contain nitrogen, bound with other carbons to a sugar. Certain plant and animal enzymes can remove the sugar, freeing hydrogen cyanide, which poisons the energy-producing mitochondria in all cells. Probably all plants can produce cyanogenic compounds, but they are most common in legumes (for example, bird's-foot trefoil) and the fruits of plants in the rose/apple family (Rosaceae); they have the odor of almonds.

Terpenoids. Terpenoids are the second-largest group of secondary compounds (fifteen- to twenty-thousand known). They are incredibly diverse in structure and activity, even though they all originally derive from a simple molecule called isoprene. Most monoterpenoids are **volatile** and comprise the characteristic odor of conifers and mints. Some volatile terpenes are produced only when the plant is wounded by an herbivore. They attract predators or parasites to the plant, which then kill the damaging herbivore; this is an indirect chemical defense because it acts via a third party (the predator or parasite). Sesquiterpenoids are the largest subgroup of terpenes and include gossypol from cotton and the sticky sap of plants in the family Asteraceae, such as lettuce and goldenrod. Triterpenoids include many extremely bitter compounds, including cucurbitacin from squashes and cucumbers; some are used as insecticides. Insects cannot synthesize cholesterol, the basis of their growth hormones, and must obtain the basic terpenoid skeleton from plants. But some plants produce steroids that act as insect hormones, disrupting insect development as a defensive ploy.

volatile easily released as a gas

Phenolics. The most diverse and common secondary compounds are phenolics. Defined by possessing a benzene ring with one attached **hydroxyl**, an enormous number of structures can be called phenolic. Most of the more than twenty-five thousand known types of phenolics are good **antioxidants** and are frequently used as preservatives; in plants they prevent membrane **oxidation** and other types of oxidative damage. As defenses, various phenolics are distasteful, toxic, and inhibit digestion. When activated by light, coumarins in such plants as carrots and celery cross-link deoxyribonucleic acid (DNA) strands and halt cell division. The blue and red colors of most

hydroxyl the chemical group -OH

antioxidant a substance that prevents damage from oxygen or other reactive substances

oxidation the removal of electrons, or the addition of oxygen

An insect on a California poppy (*Eschscholzia californica*). Poppies produce alkaloids, compounds that may interfere with neurotransmitters in the animals that ingest them.

flowers are provided by **flavonoids**, oaks and tea are rich in phenolic **polymers** called **tannins**, and the odor of wintergreen is a phenolic acid (methyl salicylate).

Glucosinolates. Glucosinolates comprise a small (one hundred) group of compounds containing both nitrogen and sulfur. They, too, are good antioxidants, but they are best known as repellents. They occur primarily in the cabbage family, where they provide the distinctive odor of those foods.

Many plant enzymes serve a defensive function. Some (such as oxidases) oxidize and activate secondary compounds; many phenolics and glucosinolates are much more defensive when this has occurred. Others produce toxic **ionic** forms of various molecules, called reactive oxygen species (ROS), which damage membranes, proteins, and DNA. Others produce signals that coordinate defense responses. Chitinases digest fungal **hyphae**, and other defensive enzymes can digest bacterial cells.

Inducible Defenses

While all plants produce some chemical defenses all the time, they also increase or alter chemical defenses when attacked by microbes or animals. These are called *inducible defenses*. Many things can induce chemical defenses, including wounding (for example, tearing), insect chewing, **pathogen** attack, and wind motion.

flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

polymer a large molecule made from many similar parts

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

ionic present as a charged particle

hyphae the threadlike body mass of a fungus

Induced responses to microbes can be very specific. A given plant genotype (e.g., variety) can recognize and respond with specific defenses against particular microbe genotypes (e.g., bacterial strain) but may not respond to others. This ability has been exploited in breeding resistant crop plants and is called gene-for-gene resistance. Plants recognize potentially deadly microbes by detecting unique proteins or other molecules on the pathogens' surface. The plant's recognition device, usually a protein, eventually activates plant genes that encode the enzymes necessary to produce defensive chemicals. Phenolics and reactive oxygen species are produced at the point of infection, blocking microbial enzymes, killing microbes and the plant's own cells, and strengthening cell walls to prevent the spread of the infection. These steps comprise a strategy for stopping the infection called programmed cell death or apoptosis. The results appear as brown spots, or necrotic lesions, and the entire process from detection to lesion is called the hypersensitive response (HR). This approach to defense is shared with animal systems.

pathogen disease-causing organism

As HR proceeds, nearby plant cells produce signals that spread through the plant and generate **systemic** acquired resistance (SAR). A plant exhibiting SAR is resistant to the original pathogen as well as others. Even tissues not yet produced when the plant was first attacked are resistant once they appear. This effect superficially resembles immune responses in animals. Scientists do not know with certainty what the signal is that circulates through the plant, but evidence indicates that it is probably not a protein, as it would be in animals. Candidates include carbohydrate cell wall fragments, phenolics (salicylic acid), plant growth hormones (e.g., abscisic acid), and electrical impulses. Many defenses are induced when genes' encoding defense-production mechanisms are activated in response to a complicated web of signals.

systemic spread throughout the plant

Salicylic acid is the chemical from which aspirin is made.

Plant responses to herbivores are not as well understood. Even small amounts of damage can induce plantwide defenses and systemic resistance. HR is not a usual component of wound responses, but signals emanating from the site of damage do produce systemic resistance. There is good evidence that a fatty acid product, jasmonic acid (JA), circulates through a wounded plant, inducing chemical defenses. In tomatoes a peptide, systemin, plays a similar role. Plant responses to herbivores is often less specific than to microbes, although different insects can induce the production of different volatile defenses from the same plant. A molecule (volicitin) related to JA has been found in the **regurgitant** of insects and triggers induced responses. It appears that at least some plants can recognize their attacker via regurgitant or saliva chemistry, and induced defenses against herbivores are also probably often activated by altered gene expression.

regurgitant material brought up from the stomach

Effectiveness of Plant Defenses

While the physiological action of some plant chemical defenses is well established, and it is relatively easy to find plant chemicals that repel or poison animals or microbes, it is more difficult to demonstrate that chemical defenses benefit plants in nature, for three reasons. First, there has been repeated evolution of microbes and herbivores that can tolerate or detoxify plant defenses. Many of these plant pests can attack only the few plant species or even tissues to which they are adapted, but no plant

A woman cuts grooves into a rubber tree to extract the sap in Manguangiong, Yunnan Province, China. The compounds rubber and latex are made from the sap produced as defenses against wood-boring beetles.

species is totally protected; there has been an evolutionary response to every plant defense. This dynamic process, in which two species (for example, plant and insect) influence each other's evolution reciprocally, is called coevolution.

Second, many scientists believe that producing defenses may be costly. Costs may include using materials (for example, sugars) for defense at the expense of growth or reproduction, a risk of poisoning one's self, or incompatibility with other life functions (for example, some nectars contain defensive chemicals and are toxic to bees). If so, then selection to reduce costs may counter selection for defense, leaving some plants vulnerable.

Third, the ability to produce defenses is constrained by the plant's genes and environment. If the mutations necessary to permit the development of a class of defenses (for example, alkaloids) has never arisen in a plant's evolutionary **lineage**, that defense—no matter how effective it might be—is not an option. And producing some defenses may be more difficult under some environmental circumstances. For example, low soil nitrogen can limit alkaloid production, and low light can restrict phenolic synthesis.

lineage ancestry; the line of evolutionary descent of an organism

No plant is perfectly protected in nature, even if it is deadly to some enemies. Total plant protection must involve other forces acting together with the plant's own defenses. Employing extremely effective chemical defenses (pesticides) as the only plant protection produces resistant pests that can tolerate and overcome them. This does not happen in nature; most natural plant systems are rarely decimated by pests. Many ecologists believe that in nature, plant protection derives from chemical defenses acting in combination with each other and with other pest control agents. For example, plant chemistry may help parasites or predators find and kill pests (indirect defense), or make pests more susceptible to their pathogens. Using more than one chemical defense at a time, and varying them through time, slows the rate at which a pest can evolve resistance. The complexity of nature is an important component of plant protection.

Human Use of Defensive Chemicals

Humans have exploited plant chemicals for thousands of years. Many uses derive directly from their defensive action. Nicotine was among the earliest of insecticides developed by humans, a practice that continues today with the isolation of antimicrobial and antiherbivore chemicals and eventual synthesis of **analogs**. Citrus chemistry is exploited as a mosquito repellent. Many antiseptic and antibiotic agents are derived from plants (e.g., terpenes in pine-scented cleaners).

analog a structure or thing, especially a chemical, similar to something else

The nervous system activity of some alkaloids has been exploited for recreational and religious drug use (opium, cocaine, nicotine, caffeine, and mescaline) and medicine (opium and codeine). The ability of some to block signal transmission at **neuromuscular junctions** makes them important in surgery as well as hunting tools (e.g., curare). Polyphenols have broad antimicrobial activity; they inhibit oxidative enzymes (e.g., cyclooxygenases) that cause disease, and their antioxidant characteristics are thought to prevent aging and some cancers. Much the same has been claimed for glucosinolates (cabbage family). More than 90 percent of the medicines prescribed in the twentieth century were originally plant derived, mostly involving presumed defensive chemicals. Human medicinal use of plants is based almost entirely on the action of defensive chemicals.

neuromuscular junction the place on the muscle surface where it receives stimulus from the nervous system

The quality of many foods derives from plant chemical defenses. **Tannins** are an essential flavor and color component of ripening fruits, wines, and chocolates. The distinctive flavors and aromas of plants in the citrus, cabbage, cucumber, and tomato families, among others, derive from their defensive chemistries. Apart from basic nutrition, food chemistry is largely the chemistry of plant defenses.

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

The cultural and industrial applications of plant defense chemistry are too numerous to list. Tannins preserve leather and were the original ink; plant phenols and carotenoids are important dyes; rubber and latex began as defenses against wood-boring beetles in rubber trees; jasmonic acid, a defensive signal, is the "queen of aromas" and is crucial to perfume formulation. SEE ALSO Alkaloids; Allelopathy; Coevolution; Defenses, Physical; Flavonoids; Interactions, Plant-Fungal; Interactions, Plant-Insect; Interactions, Plant-Plant; Interactions, Plant-Vertebrate; Physiology; Terpenes; Trichomes.

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Defenses, Physical

angiosperm a flowering plant

herbivore an organism that feeds on plant parts

taxa a type of organism, or a level of classification of organisms

Angiosperms and seed-bearing conifers provide a source of nutrients and habitat for large grazing mammals and birds as well as numerous species of insects and related arthropods. For many insect **herbivores**, the entire life cycle takes place on or within plant tissue. The evolutionary success of these plant **taxa**, the most conspicuous plants of our geological age, is due, in part, to their ability to adapt to a broad range of environments as well as their development of defenses against vertebrate and arthropod herbivores. Physical adaptations evolved by these vascular plants to defend against herbivores range from simple structural barriers to complex changes in anatomical form. Plant organs at which major defensive interaction with herbivores occurs include stems, leaves, and reproductive structures.

External Defenses

pubescence covered with short hairs

The leaves, stems, and aerial reproductive organs of vascular plants provide a large surface area and many opportunities for use as food or habitat by herbivores. Physical defensive adaptations are associated with plant color (controlled by tissue pigments, internal leaf structure, and the nature of the leaf surface), surface waxes, **pubescence**, the presence (or absence) of specialized glands, and anatomical adaptations involving plant shape and form.

Plant Color. Herbivorous insects sometimes use leaf and flower color as an aid in finding suitable host plants for food or for egg laying. Red foliage of cotton (*Gossypium*), cabbage (*Brassica oleracea*), and Brussels sprouts (*Brassica oleracea*, variety *gemmifera*) is discriminated against by the cotton boll weevil, imported cabbage worm, and cabbage aphid, respectively.

epicuticle the waxy outer covering of a plant, produced by the epidermis

desiccation drying

pathogen disease-causing organism

adhesion sticking to the surface of

Surface Waxes. The **epicuticle** of plant tissue is composed of surface waxes that protect against **desiccation** and often provide defense against insect attack and disease **pathogens**. Defensive waxes on plants of the mustard family (Cruciferae), such as cabbage, contain chemical compounds that repel pests such as flea beetles. The spatial orientation of waxy plates and rods on the leaves of resistant Brussels sprouts interferes with locomotion and **adhesion** by flea beetles. In some species of raspberry (*Rubus*), thick secretions of surface waxes act as a physical barrier by restricting aphids from successfully reaching the phloem with their sucking mouthparts.

Pubescence. Pubescence, the specialized epidermal hairs (trichomes) of vascular plants, plays an important physiological role in water conservation but also forms a physical barrier to use by herbivores and constitutes the last line of external defense. The sharp spines of cacti, the thorns of *Acacia*, wild rose (*Rosa*), raspberry, and the irritating hairs of stinging nettles (*Urtica*) create a painful barrier to grazing mammals and human interference. Trichomes that defend against insects and related arthropods also provide mechanical barrier protection, but some have evolved to entrap and immobilize these pests. Trichomes can interfere with insect adhesion and locomotion on the plant surface; trichomes rich in indigestible silica and lignin are nutritionally harmful and may **lacerate** the gut following ingestion. Highly specialized glandular trichomes can secrete substances toxic or repellent to insects through contact, ingestion, or inhalation. Although not defensive in the strict sense, glandular trichomes and **extrafloral** nectaries of carnivorous plants such as sundew (*Drosera*) secrete substances that not only entrap but aid in the digestion of prey arthropods.

Specialized Glands and Anatomical Adaptations. In many plant species leaves and flower buds bear nectar-secreting glands, probably to encourage visitation by ants or to attract pollinators such as bees. In cultivated cotton, adult moths of major pest species such as the cotton bollworm and pink bollworm are also attracted to the sugar-rich nectar. A wild species of cotton that lacks these glands has been used to breed nectarless varieties resistant to pest attack.

Some grain-producing plants such as corn (*Zea*) protect their seed by completely surrounding it with long and tight wrapper leaves (the husk) that interfere with penetration through the silk channel by corn earworm larvae. In cotton the flower bud is normally enclosed by three overlapping modified leaves (bracts), creating a moist, enclosed environment favored by the female cotton boll weevil for feeding and egg laying. In contrast, cotton varieties with the Frego bract condition are resistant because the narrow, twisted bracts create an exposed, unattractive environment for the weevil. An added benefit of the Frego bract trait is heightened weevil mortality resulting from greater exposure to weather extremes and natural enemies as well as improved penetration of pesticides applied by cotton farmers.

The protective star-patterned spines on the organ pipe cactus.

lacerate cut

extrafloral outside the flower

Internal Defenses

While the bark of woody perennials serves as a line of defense to most potential herbivores, some insects such as bark and ambrosia beetles can readily penetrate this barrier; their larvae feed just under the bark within the phloem tissue producing a distinctive pattern of tunnels often diagnostic for the species, for example, Dutch elm beetle. Feeding tunnels interfere with the normal transport of nutrients; disease pathogens introduced by the initial entry of the adult beetle further weaken the tree. Some species of conifers (*Pinus*) have evolved a form of hypersensitive response to bark beetle attack by increasing their production of oleoresin, effectively drowning or entrapping the insects within their brood chambers. Resin of resistant conifers is also characterized by high viscosity and rapid crystallization that further enhances its entrapping ability.

Another form of internal defense involves accelerated growth or replacement of damaged tissues to physically crush the invading pest (as in the case of cotton varieties resistant to the pink bollworm), or to restrict the passage of the invader through plant tissue, as occurs with galls produced by some plants in response to the entry of insects and mites.

Tissue strength and toughness are important internal defenses against the wheat stem sawfly, a significant pest of wheat (*Triticum*) in North Amer-

Tracks of a pine bark beetle in a cut log. While the bark of woody perennials serves as a line of defense to most potential herbivores, bark beetles can readily penetrate this barrier.

impede slow down or inhibit

abrasive tending to wear away through contact

ica. Larvae feed within the semihollow stems of the wheat plant creating tunnels that cause the stem to break or lodge, effectively reducing grain production. Some species of wild wheat have solid stems that **impede** the feeding and tunneling of sawfly larvae. This characteristic has been bred into modern wheat varieties to provide resistance to the sawfly. Other examples of plant breeders using wild relatives of crop plants to create barriers against tunneling insects by increasing the stiffness or toughness of stems include sugarcane (*Saccharum*) resistant to the sugarcane borer, zucchini squash (*Curcubita*) resistant to the squash vine borer, and rice (*Oryza*) resistant to the rice stem borer. In the case of rice, stems of resistant varieties have high levels of **abrasive** silica that causes accelerated wear of insect mouthparts, reducing feeding efficiency and limiting the number and length of tunnels within the stem. SEE ALSO Cacti; Cotton; Defenses, Chemical; Dutch Elm Disease; Interactions, Plant-Insect; Interactions, Plant-Vertebrate; Trichomes.

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Deforestation

Deforestation occurs when the trees in a forested area are cut or destroyed faster than they can replace themselves. When too many trees are cut or destroyed, a very important element is taken from nature, making it difficult for the forest **ecosystem** to maintain a healthy balance in its natural cycle. The imbalance of the natural forest cycle threatens the humans, plants, and animals that depend on the forest for food, shelter, and protection. The loss of trees also causes negative effects on the natural cycles that affect water, soil, atmosphere, and weather.

ecosystem an ecological community together with its environment

Why Does Deforestation Occur?

Deforestation can be a natural or manmade process. Natural deforestation is caused by changes in weather patterns during glacial periods, fires started by lightning, windstorms, floods, and volcanic eruptions. Forests often recover from natural deforestation.

Deforestation caused by humans often results in permanent deforestation. Even when humans were living as small bands of hunters and gatherers they were deforesting areas for hunting animals or to practice **swidden agriculture**, planting areas they had cleared and moving on after the soil was spent. Over time, population levels grew and areas of permanent agriculture were established, around which civilizations began to grow. These civilizations began intensely farming fields to meet the growing demand for food. As civilizations expanded, more land had to be cleared for fields and forests had to be cut to meet the demand for wood products. The stress on forested areas grew as pressure was exerted from both swidden and permanent agriculture. These stresses intensified in times of conflict as people were forced to use more marginal areas or to overcut forests to meet their needs.

swidden agriculture the practice of farming an area until the soil has been depleted and then moving on

The Industrial Revolution and the technology that came with it has allowed the world population to grow at an exponential rate and has helped bring about a different lifestyle, one based on consumerism and sustained economic growth. The end result is that the last remaining areas that still have extensive forest cover, especially tropical forests, are being cut to satisfy unsustainable human consumption patterns and economic growth models. At the turn of the twenty-first century, more than one-half of the forests that once covered the globe were gone, with much of the cutting occurring over the last decades of the twentieth century.

Effects of Deforestation

The effects of deforestation can be both local and global. In the local forest ecosystem, trees, water, soil, plants, and animals are all dependent on one another to keep healthy. When trees are cut this natural balance is upset and the important functions that trees perform such as holding the soil in place, protecting groundwater, and providing food and shelter for plants and animals cannot take place. Overcutting forests and the disruption of the forest ecosystem are causing erosion of soil, the drop in **water tables**, loss of biodiversity as plant and animal species become extinct, loss of soil fertility, and the silting up of many water bodies. When the process continues for a long period of time or over a large area there can be total environmental collapse. Parts of the world that are now desert, such as Syria, Iraq, and Lebanon, were once covered with healthy forests.

water table level of water in the soil

Deforestation, slumping, and soil erosion in Papua New Guinea's Star Mountains caused by a combination of mining and heavy tropical rainfall.

hydrological cycle movement of water through the biosphere

transpiration movement of water from soil to atmosphere through a plant

precipitation rainfall

desertification degradation or dry lands, reducing productivity

Globally the effects of deforestation are more difficult to see. Forests play an important part in the greater natural cycles that make and affect the weather and that clean the air in our atmosphere. They keep the **hydrological cycle** healthy by putting water back into the atmosphere through **transpiration**, making clouds and rain. They also capture carbon dioxide produced by the burning of fossil fuels from the atmosphere, replacing it with oxygen and thus reducing the risk of global warming. If too many forests are cut these important functions cannot be carried out. The result could be less rain, higher temperatures, and more severe weather patterns in many regions of the world.

Local and global effects of deforestation are beginning to have devastating consequences. Some areas in West Africa, for example, are already feeling the effects of lost **precipitation**, higher temperatures, and increased **desertification**. Other areas, like Venezuela, have experienced devastating floods due to treeless slopes being unable to catch the rain from heavy storms, sending it rushing into valleys. All of these problems impact the environment, but they also take a heavy toll on humans.

Alternative Strategies to Deforestation

There are several things that can be done to decrease deforestation and to offset its negative effects. Many communities are trying to reduce the burden placed on forests by instituting recycling programs and by using alternative materials like plastics in place of wood. In business, companies have begun to use wood products that come only from certified renewable forests that are carefully managed to ensure that they are cut in a sustainable way. Alternative methods of agriculture, such as agroforestry and **permaculture**, promote the use of trees and the diversification of crops to reduce the stress placed on forests by large-scale agriculture. Protecting forests by creating parks and reserves is another strategy to keep forest resources intact. For those areas that are already devastated, great efforts are being made to replant once-forested lands with native species.

permaculture agricultural practices that avoid plowing and replanting (from "permanent agriculture")

Other efforts are aimed at changing our ideas about the value of forests. Economists are now trying to calculate the true value of the forest as an ecosystem and the benefits it gives as a whole, not only the value of cut logs. This reevaluation will help us make more informed choices about how we use forest land. All of these efforts have helped reduce the burden on the forests, but cutting continues unsustainably. Without the cooperation of all humans to create alternative strategies to deforestation, it will continue with terrible results for the health of our planet. SEE ALSO BIOME; CONIFEROUS FORESTS; DECIDUOUS FORESTS; DESERTIFICATION; ECOSYSTEM; FORESTRY; HUMAN IMPACTS; RAIN FORESTS.

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Dendrochronology

Trees and other woody plants grow by covering themselves with a new layer of tissue every year. When seen in a horizontal section, such wood layers appear as concentric tree rings, familiar to anyone who has looked at a tree stump. Because tree growth is influenced by the environment, tree rings are then natural archives of past environmental conditions. For instance, trees grow less when climate conditions are less favorable, producing narrower rings. The study of past changes recorded by wood growth is called dendrochronology.

Besides determining tree age, dendrochronological information has been used in four major fields of scientific research:

- reconstruction of climatic factors that control average wood growth from year to year (such as **precipitation**, temperature, air pressure, drought severity, sunshine)

precipitation rainfall

Southern yellow pine tree rings, natural archives of past environmental conditions.

- dating of abrupt events that leave permanent scars in the wood (fire, volcanic eruptions, earthquakes, insect defoliations, and hurricanes, for example)
- dating of archaeological wood (such as the pueblos of the American Southwest, churches, bridges, and paintings in Europe)
- the calibration of the radiocarbon time scale over the Holocene epoch, covering the last ten thousand years.

The application of tree-ring dating to archaeology is indeed closely linked to the development of dendrochronology as a modern science, a process that began in the early 1900s at the University of Arizona under the direction of Andrew Ellicott Douglass, an astronomer who first established and demonstrated the principles of tree-ring dating.

Most tree-ring samples consist of pencil-shaped cores drilled from the lower stem, allowing an estimate of wood growth without cutting the tree down. So-called increment borers used for coring allow for nondestructive sampling because they leave only a 5 millimeter-wide hole, and such small injury can be readily managed by a healthy tree. (As an analogy, extracting an increment core is likely to affect a mature tree's vigor as much as drawing a blood sample is likely to affect an adult animal's health.)

Dating and Cross-Dating

Tree-ring dating is the assignment of calendar years to each wood growth ring. This requires more than simply counting visible rings, because not every growth layer is always present or clearly noticeable, especially in very old trees. When only one or two trunk **radii** are available per tree, the chance of dating errors is greater than when examining entire cross-sections. To ensure dating accuracy, ring patterns from many different trees of the same species and location are matched with one another. This allows the creation of a master chronology for this location. This cross-dating exercise, which is similar in principle to matching fingerprints or deoxyribonucleic acid (DNA) sequences, is first done visually under a binocular microscope using 10 to 30 power magnification. Once a tree-ring sample has been properly **surfaced**, that magnification is high enough to distinguish individual wood cells. After measuring the thickness of each ring, cross-dating can be verified using specialized numerical procedures. While numerical cross-dating is based on alternating patterns of narrow and wide rings, visual cross-dating can incorporate other anatomical elements as well, such as the proportion and color of earlywood and latewood within individual rings.

radii distance across, especially across a circle (singular = radius)

surfaced smoothed for examination

Cross-dating has found other important applications in dendrochronology. Once a (master) tree-ring chronology is established, a wood sample from the same species and area can be accurately dated by matching its ring-width patterns against the master. This procedure is commonly used in archaeological and historical investigations to date wood material, **artifacts**, and structures. In addition, as wood samples from older living trees are cross-matched against those from historic and prehistoric times, the length of the master chronology can also be extended farther back in time, a process that has allowed the development of tree-ring chronologies for the last ten thousand years, over the entire Holocene epoch.

artifacts pots, tools, or other cultural objects

The final tree-ring chronology is derived from the combination of all tree-ring samples into a single, average time series, which summarizes short- and long-term historical patterns for that species and site. Tree growth varies on multiple time scales, from interannual to interdecadal, and various numerical methods have been proposed to preserve (or discard) this information in the final tree-ring chronology. Such methods are grouped under the term *standardization* in the dendrochronological literature, and they are intended to minimize changes in growth rate that are not common to all trees. For climatological reconstruction, the final tree-ring chronology is statistically calibrated against instrumental records of climate, such as precipitation and temperature, to identify the main climatic signals present in the tree-ring record. The relationship between tree growth and climate is then extrapolated back into the past, and climatic changes are estimated from the tree-ring chronology itself. Because of the long life of many tree species, dendrochronological records tell of climate conditions occurring each year over hundreds, sometime thousands, of years, whereas instrumental weather records are commonly limited to the last decades, and seldom exceed one hundred years.

Tree-ring chronologies have been developed from a number of species in all continents where trees exist. In the western United States, most tree-ring records are derived from conifers, because they are very common, reach old ages, and, as softwoods, they are easier to sample than hardwoods. However, not all trees are equally suitable for dendrochronological studies. In temperate, high-latitude and high-elevation climates, wood growth is usually constrained to the warm season, and tree rings are easily recognizable. Cross-dating is easier when year-to-year variability of tree growth is higher, because this causes a greater number and degree of pattern differences in tree-ring series. When ring widths are less variable, common, climatically influenced patterns are more difficult to discern. Site conditions are therefore very important in dendrochronological studies because they affect tree-ring variability, which is an expression of the sensitivity of tree growth to climate. Other factors being the same, trees growing in difficult environments—on steep, rocky slopes, at the latitudinal or altitudinal edge of their natural range—attain greater age, grow more slowly, and show higher year-to-year changes than trees of the same species found in more **mesic** sites, on flat terrain, and/or deeper soils.

mesic of medium wetness

To date, tree-ring studies of tropical trees have been limited by the fact that wood growth layers are not visually identifiable, especially in species found at low elevations. Anatomical features and the lack of pronounced seasons allow wood growth in tropical lowlands to occur throughout or erratically during the year, making the identification of synchronous growth patterns among trees a difficult task. Even outside the tropics it is not always possible to reliably cross-date tree-ring patterns among individuals of the same species and site. A notable example is the world's tallest tree, the California coast redwood (*Sequoia sempervirens*), whose rings are not uniform around the stem. This causes different radii from the same tree to include a widely different number of rings, which prevents the development of a reliable tree-ring chronology. Such ring discontinuities are species specific and apparently unrelated to climate. SEE ALSO FORESTRY; PALYNOLOGY; RECORD-HOLDING PLANTS; TREES; WOOD ANATOMY.

Franco Biondi

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de Saussure, Nicolas-Théodore

Swiss Botanist
1767–1845

Nicolas-Théodore de Saussure was one of the early founders of plant **physiology**. He introduced new and rigorous experimental methods to the study of plants, and his work helped to improve the science of botany.

physiology the biochemical processes carried out by an organism

De Saussure was born in Geneva, Switzerland, on October 14, 1767. His father, Horace-Bénédict de Saussure (1740–1799), was also a scientist and he supervised his son's early experiments. Nicolas-Théodore accompanied his father on many expeditions to the tops of mountains to study the composition and density of air, and he made many weather and air measurements on these trips with his father in the Alps. This research led to his appointment as a professor of mineralogy and geology at the Geneva Academy.

At this time de Saussure had become interested in plant physiology, particularly in the way that plants use air. In 1804 he published his most famous work, *Recherches chimiques sur la végétation.* This collection of classic research papers introduced a new scientific method to the study of botany. His experiments were very carefully designed to address specific questions rather than to just make a series of observations. He also carefully controlled the experiments and repeated them to make sure his results were accurate. His detailed method of experimenting became the foundation for current plant science.

With this new scientific approach, de Saussure was able to demonstrate conclusively what others had long suspected. His first experiments concerned photosynthesis and respiration in plants. In one experiment, he enclosed plants in glass containers and used these containers to control the level of carbon dioxide available to the plants. After placing the plants in the light for a few hours, he measured changes in air composition in the containers and carbon accumulation in the plants. In this way, he showed that the plants had taken up the carbon dioxide and given off oxygen. In addition, he showed that carbon dioxide came from the air, not from water, as some other scientists believed. This and other similar experiments using different concentrations of oxygen and carbon dioxide and different light conditions helped him understand the basis of photosynthesis: that plants in the light are able to fix carbon in their tissues while giving off oxygen. He also correctly believed that plants used oxygen to respire in the same way as animals. He had first noted this need for oxygen in germinating seeds and plants grown in the dark. These beginning studies of respiration and photosynthesis and his later studies of plant nutrition became part of the new scientific study of plant physiology.

After this initial work, de Saussure went on to study the content of fruits and seeds and to use the ash of burned plants to examine other nutrients and minerals that plants required. Among other discoveries, he showed that plants take up nutrients from the soil selectively. His life work became a large survey of plant nutrition and, at the same time, it established a higher standard of plant scientific method. By the time de Saussure died in Geneva on April 18, 1845, he had received many honors and had become a member of many European scientific societies. SEE ALSO ATMOSPHERE AND PLANTS; HALES, STEPHEN; PHOTOSYNTHESIS, CARBON FIXATION AND; PHYSIOLOGIST; PHYSIOLOGY, HISTORY OF.

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Desertification

sterile unable to support life

mitigation reduction of amount or effect

encroachment moving in on

Human survival and prosperity are dependent ultimately on the productivity of the lands on which populations reside. In many parts of the world, however, previously productive lands have become less fertile or completely **sterile**, failing to meet the basic needs of local populations. Desertification has widely been recognized as one of the several major global environmental problems since the 1970s. According to the United Nations Environmental Programme, drylands that are susceptible to desertification account for more than one-third of the world land area and support more than 20 percent of the global human population. As the rapid growth of the human population continues, demands for resources from these fragile environments increase as well. Therefore, understanding the scope, causes, and mechanisms of desertification and developing sound and effective management and **mitigation** plans are extremely important for maintaining the ecological, socioeconomic, and political stability of both the dryland areas and the entire world.

Degradation and Loss of Productivity

The term *desertification* was first used by two French ecologists: L. Lavauden in 1927 and A. Aubreville in 1949, who then eyewitnessed the land degradation occurring in north and west Africa. Since then, more than one hundred definitions have appeared in the English literature. *Desertification* sometimes has been used interchangeably with *desertization*, which refers to desert **encroachment** into previously nondesert areas driven by human activities. A widely used definition for desertification is land degradation in arid, semiarid, and dry subhumid regions due to human activities and climate variations, which may lead to the permanent loss of land productivity. This definition was accepted at the United Nations Conference on Desertification in 1977, and later adopted by the Earth Summit, the United Nations Conference on Environment and Development in 1992, and the Intergovernmental Convention to Combat Desertification in 1994.

WORLD DISTRIBUTION OF DRYLANDS, 1996

Bioclimatic Zones	Extent (in thousands of square kilometers)	Percentage of World Land Area	P/PET Ratio*
Dry-subhumid land	12,947	9.9	0.45–0.65
Semiarid land	23,053	17.7	0.20–0.45
Arid land	15,692	12.1	0.05–0.20
Total drylands susceptible to desertification	51,692	39.7	
Hyperarid land (extremely harsh environment and thus not susceptible to desertification)	9,781	7.5	< 0.05
Total world dryland area	61,473	47.2	

* P is the mean annual precipitation, and PET is the mean annual potential evapotranspiration, which is a combined term for water lost as vapor from soil surface (evaporation) and from the surface of plants mainly via stomata (transpiration). P/PET ratio is also called aridity index (I) and is often used to classify bioclimatic zones. Smaller values of the ratio correspond to drier areas.

SOURCE: Data from United Nations Environmental Programme, 1992; adapted from H. N. Le Houérou, "Climate Change, Drought, and Desertification," *Journal of Arid Environments* 34 (1996): 133–85.

DESERTIFICATION EXTENT AND SEVERITY IN WORLD REGIONS, 1995

Region	Total Dryland Area (in thousands of square kilometers)	Desertified Area (in thousands kilometers)		
		Light and Moderate	Strong and Extreme	Total Area of Desertified Land
Asia	16,718	3,267	437	3,704
Africa	12,860	2,453	740	3,193
Europe	2,997	946	49	995
Australasia	6,633	860	16	876
North America	7,324	722	71	793
South America	5,160	728	63	791
Total	51,692	8,976	1,376	10,352

SOURCE: Data from D. S. G. Thomas, "Desertification: Causes and Processes." In *Encyclopedia of Environmental Biology,* Vol. 1, edited by W. A. Nierenberg (San Diego: Academic Press, 1995), 463–73.

Desertification may be viewed as the worst form of land degradation, the general process of declining soil fertility, impairing **ecosystem** structure and function, decreasing biodiversity, and diminishing economic viability. After an ecosystem is severely desertified, its full recovery may not be achieved even during relatively moist conditions without intensive rehabilitation efforts. Natural deserts, without human disturbances, are healthy and relatively stable ecosystems that support a variety of life forms—sometimes spectacular—like the saguaro in the Sonoran Desert. The simplistic view that desertification is a process that transforms nondesert lands into desert-like lands may thus be too superficial and misleading. Also, deserts do emerge independent of human activities, and the term *aridization* refers to this natural development of deserts through evolution of drier climates, which takes place much more slowly than desertification.

ecosystem an ecological community together with its environment

Causes of Desertification

Human abuses of the land (e.g., overcultivation, overgrazing, and **urbanization**) are the primary causes for desertification, whereas adverse climate variations (e.g., droughts) may accelerate or trigger the process. By drastically reducing or destroying vegetation cover and soil fertility, human activities can result in desertification without drought, but not vice versa. For example, overgrazing reduces both productivity and biodiversity of grasslands and can lead to a grassland-to-shrub land transition. Overcultivation completely destroys natural vegetation and can eventually exhaust soil resources. In both cases, human activities can transform drylands into unproductive wastelands through the processes of soil erosion (by wind and water), **salinization**, and **alkalinization**.

urbanization increase in size or number of cities

salinization increase in salt content

alkalinization increase in basicity or reduction in acidity

Desertification often is a result of the interactions between human and climate factors. Since human actions are tied to many social, economic, political, and environmental processes, the relative importance of major causes for desertification varies from one region to another. For example, the most dominant cause for desertification in China is overcultivation, but in north Africa and the Near East it is overgrazing. Besides droughts, global climate change may also affect desertification. Studies have suggested that global warming may reduce soil moisture over large areas of semiarid grasslands

CAUSES OF DESERTIFICATION IN WORLD REGIONS, 1996

Regions or Countries	Overcultivation	Overstocking	Fuelwood Collection	Salinization	Urbanization	Other
Northwest China	45*	16	18	2	3	14
North Africa and Near East	50	26	21	2	1	–
Sahel and East Africa	25	65	10	–	–	–
Middle Asia	10	62	–	9	10	9
United States	22	73	–	5	N/A	–
Australia	20	75	–	2	1	–

* The numbers are in percentage of the total desertified area in the corresponding region.

SOURCE: Data from H. N. Le Houérou, "Climate Change, Drought, and Desertification," *Journal of Arid Enviroments* 34 (1996): 133–85.

and thus increase the extent of desertified lands in North America and Asia. The possible effects of climate change on desertification, however, seem much smaller than the impact of land use activities by humans.

Dry-subhumid, semiarid, arid, and hyperarid areas together form the world drylands, covering as much as 47 percent of the total land area. Dry forest, grassland, and shrub land ecosystems are found in drylands except in hyperarid land (the true desert), which experiences extreme dry conditions and usually seems lifeless (e.g., central Sahara and the Namib Desert of Africa, the Hizad on the Arabian Peninsula, the Taklimakan and Turpan Depressions in central Asia, and Death Valley in the United States). Desertification occurs primarily in all drylands except hyperarid lands because climatic and ecological conditions make them more susceptible to land degradation than more humid regions. It is hard for hyperarid lands to become more desertlike, and thus they are usually excluded from the consideration of desertification.

Desertification has been occurring at an astonishing rate over six continents. Most of the desertified lands are found in Asia and Africa, while the problem also has become significant in Europe, Australasia, North America, and South America. Approximately 25 percent of the irrigated land (3 percent of the drylands), 50 percent of the rain-fed cropland (9 percent of the drylands), and 75 percent of the rangeland (88 percent of the drylands) have been desertified to different degrees. Although the accuracy of estimating the exact extent and rate of desertification needs to be improved with the aid of advanced technologies such as satellite remote sensing and geographic information systems (computer systems for storing, retrieving, and manipulating spatial or geographic data), there is little doubt that extensive areas of the world's drylands have increasingly experienced some form of chronic land degradation since the early 1900s.

Desertification has affected more than one hundred countries and resulted in profound ecological, social, and economic consequences throughout the world. Combating desertification is an urgent and grand challenge facing humanity today. Global efforts and local solutions are both needed. Preventive and rehabilitation measures must be undertaken simultaneously based on scientific findings and socioeconomic considerations. SEE ALSO Deserts; Global Warming; Human Impacts.

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Deserts

Desert **ecosystems** are characterized by an extremely arid, arid, or semiarid climate, low relative humidity, high air and soil temperatures, strong winds, high solar radiation, low **precipitation** levels, extended drought periods, soils low in organic matter, low net primary productivity, and a spatially patchy distribution of vegetation and soil resources. In them, water is the predominant controlling factor for most biological processes; precipitation is highly variable and occurs as infrequent and discrete events throughout the year; and precipitation events are highly unpredictable in both space and time. Desert ecosystems may be classified into three groups based on annual precipitation: extremely arid (less than 60 millimeters), arid (60 to 250 millimeters), and semiarid (250 to 500 millimeters). The plant communities of arid lands expand and contract in accordance with alternating wet and dry periods as well as with **anthropogenic** activities that contribute to desertification (also known as land degradation). While arid ecosystems occur on all continents in both hot and cold environments, this article will not focus on polar deserts.

ecosystem an ecological community together with its environment

precipitation rainfall

anthropogenic human-made

Distribution of Deserts Worldwide

Earth's major deserts lie within the tropics of Cancer and Capricorn where stable, high atmospheric pressure creates an arid climate at or near latitudes 30°N and 30°S. Deserts are generally located in the interior of large continents. Continental deserts are separated from ocean moisture by large distances or **topographic** barriers, such as large mountain ranges, which create a rainshadow. Deserts may also be situated on the west coast of large continents adjacent to cold ocean currents, which draw moisture away from the land. Subtropical deserts, such as the Mojave Desert of California, lie within the latitudes of 30°N and 30°S. Cool coastal deserts, including the Peruvian Atacama Desert, occur where cold offshore currents generate high atmospheric pressure and large masses of dry air, which create arid conditions upon their descent. Rainshadow deserts, including the Great Basin Desert in the United States or the Gobi Desert in Mongolia, occur where a topographical barrier such as a mountain range interrupts the flow of moist oceanic air. As moisture-laden air masses travel inland, they are deflected upward on the windward side of a mountain range, lose their moisture, and descend as dry air masses on the leeward side of the mountains. Continental interior deserts, such as the Great Sandy Desert in Australia, occur far from marine moisture.

topographic related to the shape or contours of the land

A desert plant community in Guadalupe Mountains National Park in Texas.

Plants in the Desert Environment

In order to understand the ways in which plants have adapted to arid lands, it is essential to consider the physical environment. Of all the abiotic constraints imposed on plant activity—high air temperatures, extremely high soil temperatures, high winds, intense solar radiation, and limited moisture—high temperatures and limited water are the two factors that severely limit plant growth. Summer air temperatures in the Sonoran Desert in Arizona may reach 40°C during the day but drop to 15°C at night. Soil temperatures may reach 80°C or higher. High temperatures generally are accompanied by strong winds in coastal deserts, such as the Atacama in South America and the Namib in Africa, as well as in continental deserts, including the Chihuahuan and Sonoran in the United States. As well as producing spectacular dust storms and dust devils (small whirlwinds containing sand or dust), wind also **abrades** and **desiccates** desert plants.

abrade wear away through contact

desiccate dry out

Water is the single-most limiting factor to the growth and productivity of desert vegetation. The highly sporadic nature of desert rainfall creates a pulse-reserve system of water and nutrient availability that influences many biological processes, especially plant productivity. In the Chihuahuan Desert of New Mexico, gentle winter rainfall penetrates deep into the soil profile and provides most of the moisture for the growth of perennial shrubs, such as creosote bush and mesquite. In contrast, the high-intensity, brief summer thunderstorms provide minimal water for plant growth because most of the water runs off of the soil surface. Many plant species take advantage of rainfall immediately and grow rapidly following precipitation events, then slow their growth when soils dry and moisture once again becomes limiting.

Second only to moisture, the availability of soil nutrients, primarily nitrogen and phosphorus, limits plant productivity in deserts. Nitrogen is the key limiting nutrient in North American deserts, phosphorus is most limiting in Australian deserts, while nitrogen, phosphorus, and potassium are limiting in sand dune communities in Africa's Namib Desert. Soil nutrients and organic matter tend to be concentrated in the upper 2 to 5 centimeters of soil with the greatest amounts underneath the canopies of individual desert shrubs in "islands of fertility." These resource islands harbor greater concentrations of water, soil nutrients, and microorganisms than adjacent soils.

Certain plant species, such as creosote bush, are often referred to as nurse plants. Nurse plants effectively reduce high-incident solar radiation and high temperatures under their canopies and create ideal sites for seed germination and seedling growth. The concentration of limiting resources in islands of fertility or under nurse plants generates a spatially patchy distribution of vegetation across the desert. Competition for water maintains this spacing of plants. While this phenomenon has been most studied in U.S. deserts, it occurs in arid lands worldwide.

MAJOR DESERTS OF THE WORLD

North America: Great Basin, Sonoran, Mojave, Baja California, Chihuahuan

South America: Patagonian, Puna, Monte, Chaco, Espinal, Peruvian-Chilean, Atacama

Asia: Gobi, Takla Makan, Iranian, Thar, Syrian, Arabian, Sinai, Negev

Africa: Sahara, Sahel, Somalian, Namib, Karoo, Kalahari, Madagascar

Australia: Great Sandy, Gibson, Great Victoria, Arunta, Stuart

Desert Soils

Hot deserts exhibit generally similar soil types. Immature and alkaline with weakly developed **soil horizons**, desert soils are dry most of the year, and poor in soil organic matter, nitrogen, and phosphorus, but are rich in inorganic ions, carbonate, and gypsum. The main soil orders of hot deserts are Entisols, soils without well-defined layers that are formed from recently exposed rock, and Aridisols. Aridisols, exclusive to arid regions, contain two dominant suborders: Orthids and Argids. Orthids are young calcareous and **gypsipherous** soils with a caliche (or calcium carbonate hardpan) within 1 meter of the soil surface. The thickness of the caliche layer has been correlated with the size of creosote bush shrubs in Arizona's Sonoran Desert: the thicker the layer, the smaller the shrubs. Argids are older soils and lack the carbonate hardpan layer, but are clay-rich and may be good agricultural soils when water is available.

soil horizon distinct layers of soil

gypsipherous containing the mineral gypsum

Plant Adaptations to the Desert Environment

Desert plant species show various physical, physiological, and phenological (timing of growth and reproduction) characters that enable them to survive and grow in arid, nutrient-limited environments. Some plants, such as summer and winter desert **ephemerals**, restrict all growth and flowering to periods when water is available. They are able to withstand droughts and high water stress because their underground rhizomes or bulbs remain **dormant** during the dry season. In extreme droughts, desert ephemerals may remain completely dormant, eliminate reproduction, or limit growth to the vegetative phase. Other species, such as the California poppy and other

ephemerals plants that bloom and die back within a short period

dormant inactive, not growing

Sand dunes in the Gobi Desert of Mongolia.

desert annuals, complete their entire life cycle during the rainy season. Their long-lived seeds germinate only under suitable environmental conditions. As a result, they respond to the pulse-reserve system of resource availability, showing high rates of primary production in favorable years and minimal, or no production, in drought years. Ephemerals and annuals, while showy, produce minimal **biomass**.

biomass the dry weight of a living organism

In deserts worldwide, perennial shrubs and subshrubs, such as the creosote bush and jojoba, produce most of the desert plant biomass. These species limit water loss and reduce heat loads at the leaf surface by limiting the surface area to many small single, dissected, or compound leaves covered with a waxy cuticle or leaf hairs. Most shrubs have canopies with a compact globe or inverted cone shape. This **morphology** allows water to funnel directly to the plant roots and reduces the amount of surface area that is exposed to sunlight. Perennials have a large root-to-shoot ratio, and most roots are distributed in the soil in one of two ways. The roots may be confined to the upper meter of the soil profile and fan out horizontally from the base of the shrub, enabling shrubs access to even the slightest rainfall. Alternatively, the roots may extend deep into the soil profile—up to 12 meters with mesquite—and allow plants to obtain water that is stored at these depths. As with other desert plants, perennials may also limit or suppress flowering and fruiting in years of extreme drought.

morphology shape and form

Perennials are able to remain metabolically active at very low soil- and plant-water potentials, high internal water deficits, and high temperatures. They have sensitive regulation of leaf **stomata** as a function of internal and external conditions, including water stress, temperature, atmospheric humidity, and light intensity. Most shrub species acquire carbon throughout the C_3 photosynthetic pathway, despite the fact that the alternative C_4 pathway is thought to increase the amount of carbon gain per unit of water used (water-use efficiency [WUE]). The only desert perennials that have the C_4 pathway are the halophytic (salt-tolerant) species, such as tamarisk, short-lived summer active perennials, and most grasses.

stomata pores that open to allow gas exchange and close to prevent water loss

Cacti, common to deserts, show unique adaptations to the desert environment. They have shallow, horizontally extended root systems, an upright, ribbed trunk that reduces the midday heat and solar radiation load and water storage within their trunks. Saguaro cacti, located near Tucson, Arizona, expand and contract like an accordion depending on the moisture conditions. In wet years the cacti are plump and green, but in dry years they are slim and yellow-green in color. Because cacti lack typical broad leaves, the overall green coloring derives from the photosynthetic trunk. Over evolutionary time, cactus "leaves" have been reduced to hairlike spines that reflect solar radiation or spikelike spines that protect the plant from **herbivores**. Other noncactus species, such as ocotillo and the boojum trees native to Baja California, produce photosynthetically active leaves only in wet years and limit photosynthesis to the stems when drought prevails. Cacti and other **succulent** species obtain carbon through the **crassulacean acid metabolism** (CAM) photosynthetic pathway. CAM photosynthesis allows the cacti to open their stomata only at night in order to reduce water loss. SEE ALSO CACTI; DESERTIFICATION; PHOTOSYSTHESIS, CARBON FIXATION AND.

Anne Fernald Cross

herbivore an organism that feeds on plant parts

succulent marked by fleshy, water-holding leaves or stems

crassulacean acid metabolism a water-conserving strategy used by several types of plants

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Dicots

morphological related to shape

adventitious arising from secondary buds, forming a fibrous root system

vascular related to transport of nutrients

angiosperm a flowering plant

legumes beans and other members of the Fabaceae family

phylogenetic related to phylogeny, the evolutionary development of a species

The dicots (short for dicotyledons) have long been recognized as one of two major groups or classes (class Magnoliopsida) of flowering plants (division Anthophyta or Magnoliophyta), the other major group being the monocots (monocotyledons; class Liliopsida). The dicots have traditionally been distinguished from monocots by a suite of **morphological** and anatomical features, all of which are subject to exception, however. For example, as the name of the group suggests, most dicots possess two seedling leaves, or cotyledons. In addition, dicots often possess netlike leaf venation, flower parts in fours or fives (or multiples thereof), vascular bundles in the stem arranged in a ring, with the potential for true secondary growth, and a root system of primary and **adventitious** roots. Monocots, in contrast, have one cotyledon, parallel leaf venation, flower parts in threes (or multiples thereof), scattered **vascular** bundles in the stem, lack true secondary growth, and have only an adventitious root system. As traditionally defined, the dicots comprise approximately 165,000 to 180,000 species; the monocots are the smaller of the two groups, consisting of about 60,000 species. The dicots include all the familiar **angiosperm** trees and shrubs (though not the conifers) and many herbaceous groups, including magnolias, roses, oaks, walnuts, **legumes**, sunflowers, snapdragons, mints, and mustards. Most recent classification schemes, such as those of Cronquist, Takhtajan, and Thorne, have divided the dicots into six subclasses: Magnoliidae, Hamamelidae, Caryophyllidae, Rosidae, Dilleniidae, and Asteridae.

Although the monocot-dicot division has been recognized since the late nineteenth century, recent **phylogenetic** studies demonstrate clearly that this split does not accurately reflect the evolutionary history of flowering plants. That is, phylogenetic trees depicting historical relationships have re-

MAJOR DICOT FAMILIES

Family	Common Name	Number of Species (approximate)
Apiaceae	Parsley or carrot family	3,000
Asteraceae	Sunflower family	25,000
Betulaceae	Birch family	170
Brassicaceae	Mustard family	3,000
Cactaceae	Cactus family	2,000
Caryophyllaceae	Carnation family	2,000
Cornaceae	Dogwood family	100
Cucurbitaceae	Pumpkin family	700
Ericaceae	Heath family	3,000
Euphorbiaceae	Spurge family	5,000
Fabaceae	Pea or legume family	17,000
Fagaceae	Beech or oak family	1,000
Lamiaceae	Mint family	3,000
Lauraceae*	Cinnamon family	2,500
Magnoliaceae*	Magnolia family	200
Nymphaeaceae*	Water lily family	90
Papaveraceae*	Poppy family	650
Piperaceae*	Black pepper family	3,000
Ranunculaceae	Buttercup family	1,800
Rosaceae	Rose family	3,500

* Indicates families of traditional dicots that are now recognized as basal angiosperms, which are ancestral to both monocots and dicots.

cently been constructed for flowering plants (based on deoxyribonucleic acid [DNA] sequence data as well as morphological, anatomical, chemical, and other non-DNA characters). These diagrammatical trees indicate clearly that while the monocots form a **clade**, all of the dicots do not form a distinct group separate from the monocots. Instead, the monocots are imbedded in a clade of early branching **lineages** of flowering plants, usually referred to as magnoliids, all of which have the characteristics of the traditional dicots. These early branches of angiosperms, including the monocots, are characterized by pollen grains that have a single aperture (or line of weakness), or by pollen types that are derived from this single-aperture form.

clade a group of organisms composed of an ancestor and all of its descendants

lineage ancestry; the line of evolutionary descent of an organism

The majority of angiosperms form a distinct clade and are referred to as the eudicots (or true dicots). Eudicots are characterized by pollen grains that typically possess three apertures; no other morphological or anatomical structures that mark this group have been identified, although the grouping of the eudicots is strongly supported by analyses based on DNA sequence data.

Thus, there is no monocot-dicot split in the angiosperms. Whereas *monocot* remains a useful term, *dicot* does not represent a natural group of flowering plants and should be abandoned. It is more useful to refer to eudicots, which represent a well-marked clade of flowering plants, and to specific groups of ancient dicotyledonous angiosperms (basal angiosperms). In many ways this conclusion is not surprising. Botanists long theorized that the monocots were derived from an ancient group of dicots during the early diversification of the angiosperms. Phylogenetic trees of relationship derived from molecular data confirm this longstanding hypothesis and pinpoint the possible close relatives of the monocots.

The eudicots, containing approximately 75 percent of all angiosperm species, comprise several distinct lineages. The earliest branches of eudicots are the Ranunculales, which include the Ranunculaceae (buttercup family) and Papaveraceae (poppy family), as well as the Buxaceae (boxwood family) and Platanaceae (sycamore family). Most eudicots form a large clade, composed of three main branches and several smaller ones. The main branches of eudicots are the eurosids (made up of members of the traditional subclasses Rosidae, Dilleniidae, and Asteridae), the asterids (containing members of subclasses Asteridae, Dilleniidae, and Rosidae), and the Caryophyllales; there is no clade that corresponds to subclass Dilleniidae.

The first angiosperms that appear in the fossil record possess those characteristics typically assigned to the dicots, and both the monocots and eudicots evolved later. The eudicots can be identified in the fossil record by their three-grooved pollen as early as 110 million years ago. Following the origin of this group, it diversified rapidly, and by 90 to 80 million years ago many of today's prominent families of angiosperms were established and are clearly recognizable in the fossil record. SEE ALSO ANGIOSPERMS; EVOLUTION OF PLANTS; MONOCOTS; SYSTEMATICS, PLANT.

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Differentiation and Development

Mitotic cell division in unicellular organisms such as bacteria or yeast produces identical sister cells that are also identical to the mother cell. But in multicellular plants, sister cells are different from each other and usually also from the mother cell that produced them. These differences result from variations of gene expression in cells that are genetically identical. (The alternative hypothesis, that differentiation depends on differences in gene content in different cell types, can be discounted because differentiated cells isolated from the plant and placed in sterile culture on suitable nutrient medium regenerate entire plants that contain all the expected cell types.) The fifty or so specialized cell types of higher plants result from the operation of three developmental processes: cell polarity, asymmetric cell divisions, and positional information.

Origin of Cell Polarity

Polarity is the condition in which opposite ends of a structure are different. In biology this can apply to a cell or a tissue or an organism. Polarity in a multicellular plant exists in the first cell, the **zygote**, with the consequence that the two sister cells produced by the first division have different developmental fates.

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

intertidal between the lines of high and low tide

The best studied example is the origin of polarity in the zygote of *Fucus*, a brown alga of the marine **intertidal** zone. Eggs are released into the seawater and fertilized. Polarity is established initially by the site of sperm penetration, and in the absence of other disturbing factors the rhizoid emerges at this point. Numerous environmental gradients, however, including light, gravity, temperature, and pH, may act as final determinants of the polar axis. The zygote settles onto a **substrate**, and a rhizoidal outgrowth develops from one side of the cell. Following nuclear division, a new cell wall separates cells that have different developmental fates: a hemispherical cell that will form the **thallus**, and a rhizoidal cell that will form the holdfast.

substrate the physical structure to which an organism attaches

thallus simple, flattened, nonleafy plant body

vesicle a membrane-bound cell structure with specialized contents

The process of polar axis fixation involves a current of calcium ions moving into the cell at the site of future rhizoid emergence and the accumulation of calcium channels in the membrane at this site. Actin filaments then accumulate, and Golgi-derived **vesicles** containing cell wall precursors migrate through the cytoplasm and release their contents at the site of rhizoid formation. All these events precede division of the zygote into two cells, so that it is the zygote itself that becomes polarized.

angiosperm a flowering plant

organelle a membrane-bound structure within a cell

apical at the tip

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Use for storage and maintaining internal pressure

transverse across, or side to side

auxin a plant hormone

In **angiosperms**, the egg is already polarized at the time of fertilization. The nucleus and most of the cytoplasmic **organelles** are located near the **apical** end of the cell and a large **vacuole** occupies much of the basal (lower) half. Division of the zygote is **transverse**, separating a small cytoplasmically rich apical cell that forms all or most of the embryo from a large vacuolated basal cell that forms the extraembryonic suspensor.

It has been proposed that auxin establishes the polar axis in angiosperm embryos, as it does in *Fucus* zygotes. Movement of **auxin** through plant cells and tissues is polar from apex to base. This one-way transport is thought to depend on differential or polarized localization of membrane-associated auxin binding and transport proteins.

In the above examples, the result of cell division is the production of two cells that are visibly different and have different developmental fates. Such divisions are said to be asymmetric.

Asymmetric Cell Divisions

Asymmetric cell divisions are those in which there is unequal partitioning of cell components to the daughter cells. Examples are unequal distribution of cytoplasmic organelles, membrane components such as ion channels or pores, receptor molecules, or cell wall components. As a result of this differential inheritance of fate determinants from the mother cell, the daughter cells have different developmental fates, and this is the way that the term *asymmetric cell division* has been applied usually.

In the development of root epidermal cells of monocotyledons, cytoplasm accumulates at the end nearest the root tip, resulting in a polarized cell. This end is subsequently cut off by an asymmetric cell division, resulting in a small, cytoplasmically rich trichoblast ("hair precursor"), and a larger vacuolated epidermal cell. An outgrowth of the trichoblast develops as a root hair.

The formation of stomata, the pores that allow gas exchange between the atmosphere and internal tissues of leaves, involves both symmetric and asymmetric divisions. In most dicotyledons a developing epidermal cell divides asymmetrically to form a small triangular cell (when viewed from the surface). This cell, termed a meristemoid because it continues to divide after adjacent cells have ceased division, divides symmetrically to form two identical stomatal guard cells that form the pore, or in some species it may undergo several divisions before forming the guard cells.

Another important asymmetric division is the division of the microspore, separating a small, cytoplasmically rich generative cell that forms the male gametes from a larger vegetative cell. This is the first division in pollen development and separates two cells with different developmental fates. In mutants where this division is affected, either the division fails to occur or it is symmetric. In either case pollen development fails, indicating the importance of the asymmetric division to this process.

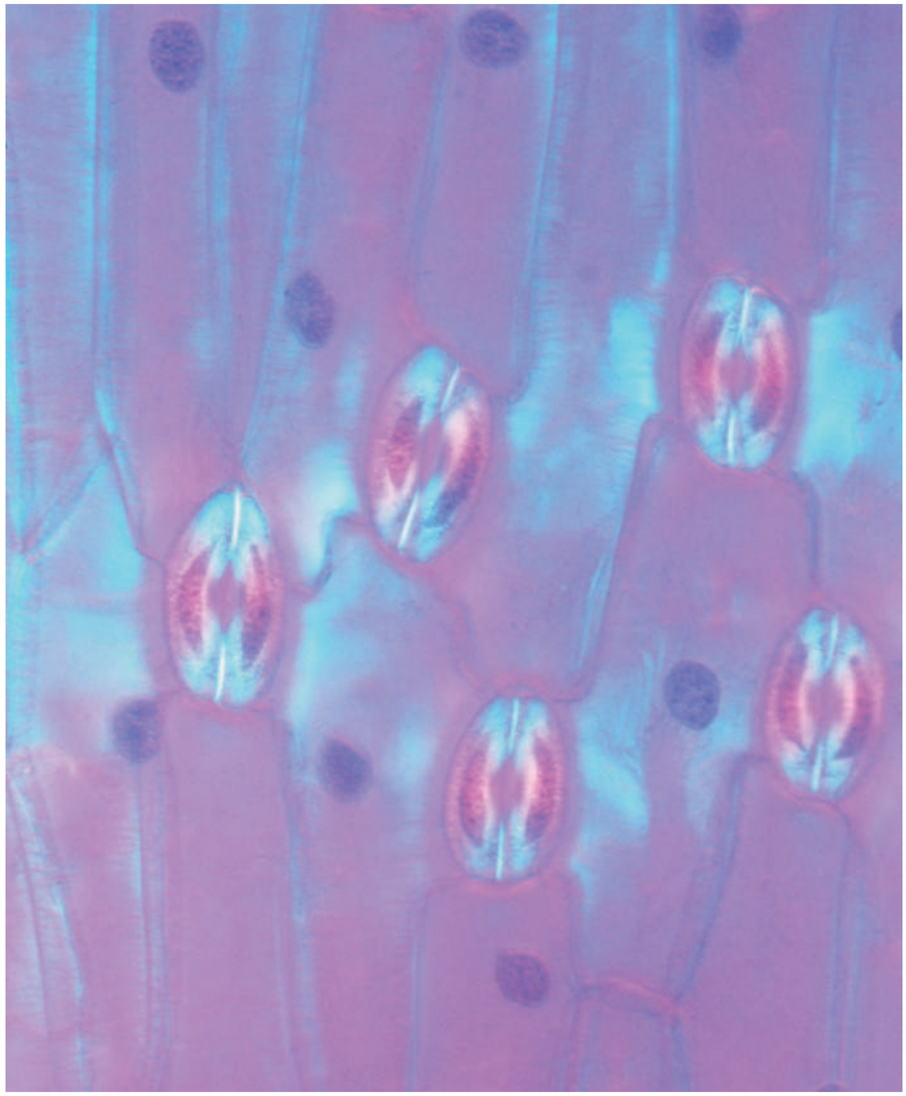
Positional Information in Cell Differentiation

The consequences of cell polarity and asymmetric divisions are to place sister cells of a mitotic division in different cellular environments, such as closer to or farther from the tip of the organ or to the inside or outside in a tissue. These cells, occupying different positions, may then be receptive to different external information, and this is the basis for the concept of positional information. Although the concept has a long history in developmental biology, it was Lewis Wolpert in 1971 who formalized it.

Positional information has been invoked to explain many developmental processes but there are relatively few in which it has been subjected to experimental analysis. One of the best examples is the development of root hairs in *Arabidopsis*. The root **epidermis** consists of files of root-hair-bearing trichoblasts alternating with files of hairless cells. Trichoblasts occupy predictable positions over the radial walls of underlying **cortical** cells. This suggests that the alternating pattern of trichoblast files is determined

epidermis outer layer of cells

cortical relating to the cortex of a plant



Stomata from a tulip leaf. The formation of stomata involves both symmetric and asymmetric divisions.

by the positions they occupy, and it has been proposed that the gaseous plant hormone ethylene is produced in the radial wall boundaries of cortical cells and activates root-hair formation. Mutants that vary in their response to ethylene confirm this suggestion, indicating that the molecular basis of positional information in this case had been identified. SEE ALSO ANATOMY OF PLANTS; EMBRYOGENESIS; GENETIC MECHANISMS AND DEVELOPMENT; GERMINATION AND GROWTH; HORMONAL CONTROL AND DEVELOPMENT; MERISTEMS; SENESCENCE; TISSUES.

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Dioscorea

Second only to potatoes in terms of world tuber production, true yams (genus *Dioscorea*) are more closely related to tulips (both are monocots) than to the sweet potato (*Ipomoea batatas*), which is also often called a yam. The genus *Dioscorea* includes around eight hundred tuberous, annual species of **twining** or **rambling habit**, mostly found in tropical regions.

twining twisting around while climbing

rambling habit growing without obvious intended direction

domesticate to tame an organism to live with and to be of use to humans

Cultivated for their starch-rich tubers, true yams were originally **domesticated** in three independent regions: Africa, Asia, and the New World. Today, yams, especially *D. rotundata*, are grown extensively throughout the tropics.

A number of *Dioscorea* species naturally produce saponins (a type of steroid). The most useful of these compounds, diosgenin, is very similar to the human sex hormones estrogen, progesterone, and testosterone. Present in the tubers at concentrations of up to 40 percent of its steroidal contents, *Dioscorea* represents a valuable source of diosgenin that is used to synthesize human sex hormones at low cost. This led to the development of the female contraceptive pill, which continues to be one of the most effective and widely used methods of birth control.

In 1952 researchers discovered that the fungus *Rhizopus* can convert diosgenin into the steroid cortisone, a human hormone. Along with hydrocortisone (also produced from diosgenin), cortisone plays an important role in medicine, particularly in the treatment of allergic reactions (such as those produced by insect bites and stings), and for reducing inflammation of the joints in patients suffering from arthritis. SEE ALSO Economic Importance of Plants; Lipids; Medicinal Plants; Monocots.

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Dutch Elm Disease

Dutch elm disease is a fungal infection of the **vascular** system of elm trees. The fungus, *Ophiostoma ulmi*, is spread from diseased to healthy trees by elm bark beetles. Fungal spores adhering to the beetles are introduced to the tree through feeding wounds in young branches. In nonresistant elms, large portions of the vascular system are infected before the tree can defend itself against the invading **pathogen**. Water transport within the tree is blocked by the fungus and the tree eventually wilts and dies.

vascular related to transport of nutrients

pathogen disease-causing organism

The fungus first appeared in the Netherlands about 1912; from there it spread across Europe, reaching the United States in 1930. At the time, the

Bark beetle tunnels revealed beneath the bark of a tree infected with Dutch elm disease.

American elm, *Ulmus americana*, was the premier urban tree, planted for its beauty, shade, and durability. Across the Midwest, this hardy, quick-growing tree was used for windbreaks as well as on the streets of new towns. As the disease spread across the nation, streets once shaded by majestic, arching elms were soon barren of trees. It is estimated that over one hundred million trees have been lost to the disease.

Early attempts at controlling the disease concentrated on killing the fungus and its **vector**. As tree spraying became frowned upon and injection of fungicides more costly, more effort has been made to breed disease-resistant elms. Several European cultivars that have been developed are not completely resistant to the disease or sufficiently cold-hardy for North America. **Hybrid** crosses of resistant Asian species with American species lack the height and characteristic form of the American elm. Selective breeding and testing of American elms has led to promising varieties such as American Liberty, Princeton, and Valley Forge, but whether any of these will be resistant to the disease as the fungus itself evolves remains to be seen. SEE ALSO BREEDING; INTERACTIONS, PLANT-FUNGAL; INTERACTIONS, PLANT-INSECT; PATHOGENS.

Craig Steely

vector carrier, usually a carrier who is not affected by the thing carried

hybrid a mix of two species

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Ecology

Ecology is the study of organisms and their relationship to the environment. The field was born in 1866 when German biologist and philosopher Ernst Haeckel (1834–1919) created the precursor to the modern word "ecology" by combining the Greek words *oikos*, meaning "home," and *logos*, meaning "study," to create the word "oecology." Haeckel used this word to summarize the concept of natural selection and the struggle for existence that English naturalist Charles Darwin (1809–1882) had outlined in his groundbreaking work on evolution, *On the Origin of Species.*

In the early twentieth century, even before the modern word *ecology* had been invented, interest in what is now called plant ecology began to grow. American botanist and ecologist Frederic Clements (1874–1945) and others conceived the idea that plants would develop in an orderly succession of formations from pioneer species to a well-defined and stable group of species called a climax community. Clements believed that plant formations were like intact organisms with a predictable pattern of birth, growth, and death. Clements's ideas were quickly challenged. American botanist and plant ecologist Henry Allan Gleason (1882–1975) argued that the distribution of plants was the result of random events in the environment that combine to form an individual and possibly unique plant community. Partially in response to the rigid classification developed by Clements, British ecologist Arthur Tansley (1871–1955) in 1935 coined the word *ecosystem* to describe what he called a *quasi organism.* Tansley's concept of the ecosystem as a single physical unit containing both organisms and their environment is essentially the same to this day.

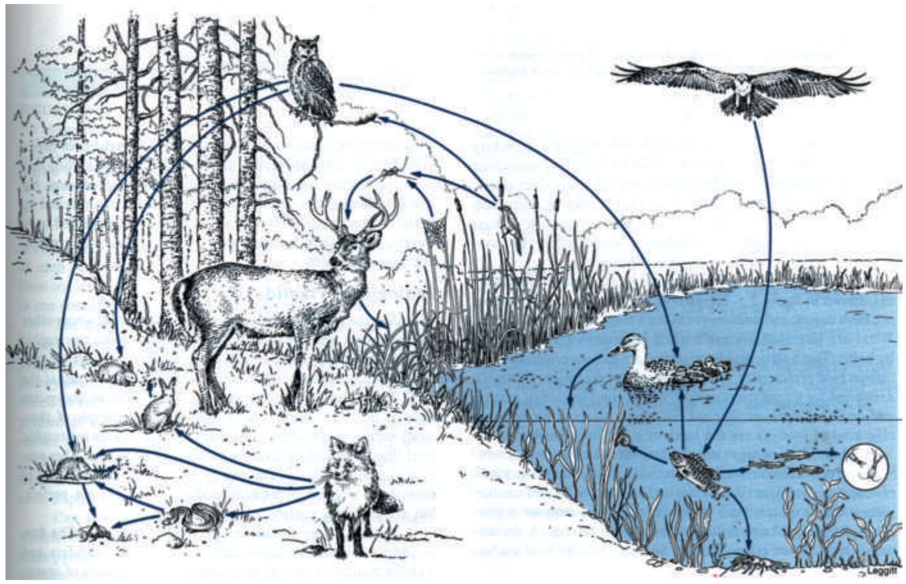
Plant Ecology

The concept of ecology may seem fairly simple, but in practice it is very complex. As the field developed, scientists soon found themselves unable to master the entire discipline, and even within the already narrowed field of plant ecology, subfields rapidly developed. Today, there are six major fields of plant ecology:

- **Population ecologists** study the relationship of individuals of one species in a given area to each other and to their environment. A population ecologist might be interested in what environmental conditions limit the northern range of black spruce trees in the Canadian boreal forest.
- **Community ecologists** study the distribution and abundance of groups of species and how they are influenced by biological and environmental factors. Community ecologists have studied the major associations of deciduous forests in the eastern United States and how the environment, in terms of climate, soils, and topography, controls this association.
- **Ecosystem ecologists** study energy and matter transport through organisms (see below). This includes studies of how nutrients, energy, and **biomass** are cycled through ecosystems. The study area for ecosystem ecologists depends on the defined ecosystem and can vary from small ponds or tiny forest plots to the entire globe. Ecosystem ecologists are today conducting politically and economically important research on the global carbon cycle.

biomass the total dry weight of an organism or group of organisms

- **Physiological ecologists** study how environmental factors such as light, temperature, and humidity influence the biochemical functioning of individual organisms. Physiological ecology and ecosystem ecology are very complementary; often ecologists have a hard time deciding if they are one or the other.
- **Landscape ecologists** study the biological and environmental factors that influence vegetation patterns observed in a landscape. Land-



Energy flow refers to the way that energy is transformed through a food chain (pictured here) containing a series of levels, including plants, consumers, predators, and decomposers.

scape ecologists may study the factors controlling the boundary between forests and grasslands.

- **Human ecologists** study the influence of human activity, both currently and historically, in controlling the distribution and abundance of organisms. Human ecology also examines the social and cultural factors that control the way humans exploit, alter, and manage the environment. Most ecological research has focused too much on natural ecosystems while pretending that humans do not exist. For example, an ecologist coming across the deciduous forest in New England today might assume that the forest always looked that way. In fact, the present pattern of forest distribution is the result of extensive human modifications by Native Americans, European colonists, and foresters.

Food Webs

In the 1950s the idea of the food web began to emerge in ecosystem ecology. Food webs and the related topics of **trophic** levels and energy flow are some of the most critical ecological concepts because they illustrate the connections between organisms that are required to maintain healthy ecosystems.

trophic related to feeding

Energy flow refers to the way that energy is transformed through a food chain containing a series of levels, including plants, consumers, predators, and decomposers. Each step in the food chain is called a trophic level (from the Greek word *trophikos*, meaning "nutrition"). Primary producers (plants, algae, and photosynthetic microbes) are the base of food chains and are the lowest trophic level. They transform energy from the Sun into sugars. Primary producers thus make their own food and are called **autotrophs**; all other organisms ultimately use the energy produced by autotrophs and are called **heterotrophs**. At the next trophic level, primary consumers (**herbivores**) eat some of the sugars produced by primary producers. Secondary consumers (predators) consume primary consumers and other secondary

autotroph "self-feeder"; any organism that uses sunlight or chemical energy

heterotroph an organism that derives its energy from consuming other organisms or their body parts

herbivore an organism that feeds on plant parts

consumers. Decomposers such as earthworms, maggots, fungi, and bacteria break down the carcasses of dead primary and secondary consumers and uneaten primary producers.

The amount of living material (biomass) and energy in food chains has a specific ordering between trophic levels. Consider a simple example of an African savanna ecosystem consisting of trees and grasses (primary producers), gazelles and zebras (primary consumers), and lions (secondary consumers). If we check the trophic levels, we will find that primary producers have the most biomass, followed by primary consumers, and then secondary consumers. The amount of energy at each trophic level will follow the same pattern. This ordering of trophic levels forms a pyramid with primary producers at the bottom followed by primary consumers in the middle and secondary consumers on the top. More energy is required at the lower levels of the pyramid because during the transfer between trophic levels energy is lost through heat and waste products.

Most ecosystems on land follow the pyramid pattern. In the ocean or other aquatic systems, the opposite pattern may at times be true: at any one time, the biomass and energy of the primary and secondary consumers may exceed those of the primary producers. This is because photosynthetic algae have a very short life span. Even though they may have a low biomass at any one time, their biomass measured over the whole year will be larger than the biomass of the consumers.

The pyramid concept of trophic levels is consistent across many terrestrial ecosystems, but in reality the interactions among organisms are much more complex than in the African example. A food web is a network of connected food chains and is used to describe community interactions. Consider a food chain in the Rocky Mountains. Small aquatic plants are primary consumers in a stream ecosystem. Arthropods and fly larvae feed on the plants and are in turn consumed by trout. Bears eat the trout. But each part of this food chain is also connected to other food chains. Birds feed on plants and fish, while bears will also feed on roots, tubers, and rodents. The complete network of these connections forms an ecosystem food web.

Food webs are usually more complex in ecosystems that have not been disturbed for a long time. Food webs in coral reefs and tropical forests have thousands of highly specific food chains. In these ecosystems, many animals are adapted to feed on one or only a few food sources. Disruption of a few elements can have serious consequences for the entire food web. By contrast, the tundra ecosystem was covered in ice until about 8000 B.C.E. In this ecosystem, there has been less time to evolve complex and specific food webs. Species tend to be interchangeable. Removal of one species or interaction does not usually seriously damage the health of the entire food web.

Advances in Ecological Research

Advances in the ecology field happen frequently. The following four examples from the late twentieth century show the breadth of the field as well as the need for ecologists to reach across disciplines.

Leaf Design. There are thousands of kinds of leaves, ranging from tiny evergreen needles to enormous tropical leaves more than fifty centimeters wide. In spite of great diversity, leaves follow a strict set of rules. Long-lived leaves, such as ten-year-old spruce needles, have a low nitrogen concentration (this means low rates of photosynthesis) and thick, dense leaves that are highly resistant to herbivores. Short-lived leaves, such as blades of grass lasting only weeks or a few months, have a very high nitrogen concentration and thin, light leaves. Almost all leaves follow this pattern and are either long-lived with low rates of photosynthesis and a high resistance to herbivores, or short-lived with high rates of photosynthesis and herbivory. Intermediate levels of all three traits are also possible. This finding, drawn from hundreds of plants all over the world, helps to explain the appearance and **physiology** of leaves and is one of the most important ecological findings in recent years.

physiology the biochemical processes carried out by an organism

Ecosystem Carbon Storage. Many ecologists wanted to know the total amount of carbon released or stored by ecosystems, but until recently, there was no way to accomplish this. Experimental meteorologists devised a method called eddy covariance to measure the amount of carbon dioxide entering or leaving an ecosystem. By adding up these numbers over the course of a day or year, ecologists can now determine if an ecosystem is storing more carbon through photosynthesis or releasing more carbon through respiration. They found that many forests are storing carbon, but that some, especially in the boreal forest, can release carbon due to slight changes in climate. This research is critical for understanding the carbon cycle and the potential for global climate change.

Impacts of Rising Carbon Dioxide. Scientists have published hundreds of research articles on the response of plants in greenhouses or special enclosures to increased carbon dioxide (CO_2) levels, but there had been no way to test the response of real ecosystems. Scientists at the Brookhaven National Laboratories developed the Free-Air CO_2 Enrichment (FACE) system. FACE uses a circle of instruments that pump CO_2 into the atmosphere to artificially increase the CO_2 levels of a real ecosystem. The increased CO_2 increased photosynthesis, supporting earlier greenhouse results showing that plants would respond to higher CO_2.

Ecology and Natural Resource Management

Beginning in the early twentieth century, ecological theories began to be seriously considered in natural resource management. Unfortunately, results were not always good. In an application of Darwinian theory, U.S. Forest Service managers believed that by clearing old, unproductive forests and replacing them with young, vigorously growing forests they would increase forest health and productivity. Instead, throughout much of the dry inland Rocky Mountains foresters created dense thickets of fire- and insect-susceptible forests. Today, guided by modern ecological research, this policy is changing to include a focus on returning fire to the ecosystem and managing forests for the health of the entire ecosystem, not just human economics. This is called ecosystem management. In large part, it was the legal, political, and social pressures exerted by nonscientist citizen activists that caused this shift in natural resource management policy.

Ecological research has been used in many other ways to improve natural resource management. Due to ecological research showing the catastrophic effects of cyanide on river ecosystems, **cyanide heap leach gold mining** is now being restricted. Ecologists showed how DDT, an insecti-

cyanide heap leach gold mining a technique used to extract gold by treating ore with cyanide cide common in much of the world during the mid-1900s, was transferred through trophic levels until it reached toxic levels in secondary consumers. Millions of birds were killed before DDT was banned in most of the world. Ecologists found that large, interconnected populations of grizzly bears were required to ensure long-term breeding success of the species and natural resource managers are now designing migration corridors to link the remaining bear populations.

In short, there are very few areas of natural resource management that are unaffected by ecology. Critical developments include:

- ecosystem management for recreation, water quality, and protection of endangered species, not just economic development
- an increased awareness of public health consequences
- attempts to reintroduce elements of ecosystems that had been removed by humans
- consideration of the complex and sometimes fragile nature of food webs before making resource management decisions.

Role of Computer Modeling

Politicians, scientists, and natural resource managers are becoming more and more interested in complicated ecological questions over large regions. For example, the economically critical and politically sensitive issue of the global carbon cycle is being answered mostly by ecosystem ecologists. Clearly, it is impossible to measure the entire Earth. Another solution is required, and computer models have filled this need.

A computer model is a system of mathematical equations that ecologists use to represent the ecosystem or problem being assessed. Models do not duplicate reality; they are simplified systems that attempt to represent the most critical processes while ignoring all the details that are impossible to measure or extremely difficult to represent with mathematics. Ecological models range from detailed treatments of gas exchange for a single leaf to carbon cycle models for the entire globe. Developing a good model of the global carbon cycle is like trying to make the simplest possible car: you strip away everything you possibly can until the car stops running. Just as in a car you could probably remove the windows and the passenger seat but not the transmission or the engine, in a global carbon model, you can probably ignore individual species and hour-to-hour weather changes but not vegetation and climate.

Computer models have an extremely significant role in ecology. In fact, because so much in ecology is so difficult to measure except for the smallest plot, models are common in every field of ecology. Models are highly useful for testing scenarios. What will happen to stream flow and fish populations if 50 percent of trees are cut in a watershed? How will elk populations change if wolves are reintroduced to a particular area? How will the introduction of small controlled fires affect the potential for larger, highly destructive fires? How will forests respond if carbon dioxide levels double in the next one hundred years? These are just some of the ways that ecological models are used. SEE ALSO BIOME; CARBON CYCLE; CLEMENTS, FREDERIC; ECOLOGY, ENERGY FLOW; ECOLOGY, FIRE;

Ecology, History of; Global Warming; Interactions, Plant-Fungal; Interactions, Plant-Insect; Interactions, Plant-Plant; Interactions, Plant-Vertebrate; Plant Community Processes; Savanna; Tundra.

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Ecology, Energy Flow

Organisms are complex biochemical machines that require a constant consumption of energy to grow, reproduce, and maintain their biological integrity. The use of energy must obey physical principles: the laws of thermodynamics. Constraints imposed by these principles have profound influence in the flow and conservation of energy and therefore the structure of an ecological community.

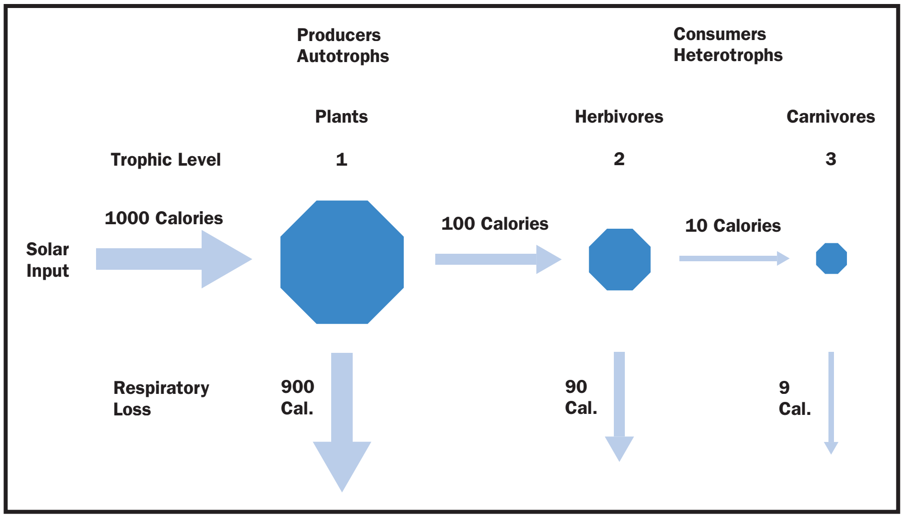
Energy from the sun powers the world's ecological communities. Solar energy is channeled into an ecological community by way of photosynthesis in green plants and many other photosynthetic microorganisms. Energy harvested by photosynthesis is used to produce plant tissue where light energy is saved as chemical energy. This chemical energy is transferred when plants are eaten by herbivores (plant-eating animals). Energy stored in herbivores can further be transferred to carnivores (animal-eating animals). This sequence of energy transfer from plants to herbivores and then carnivores is called a food chain. Along the food chain, the number of transfers for the solar energy to reach an organism defines its **trophic** level. Plants therefore occupy the first trophic level, herbivores the second trophic level, and herbivore-eating carnivores the third trophic level. A species population can occupy more than one trophic level depending on the source of energy actually assimilated.

trophic related to feeding

autotroph "self-feeder"; any organism that uses sunlight or chemical energy

heterotroph an organism that derives its energy from consuming other organisms or their body parts

Organisms can be classified into **autotrophs** and **heterotrophs** depending on the nature of energy and nutrients they use. Autotrophs, which include all the higher plants and algae, use light as their energy source and



Energy flow along the grazing food chain, assuming 10 percent efficiency at all trophic levels.

they depend completely on inorganic nutrients for their growth. Heterotrophs, which include all the animals, protocists, fungi, and many bacteria, use chemical energy for their needs and require organic compounds for their growth. Heterotrophs acquire both energy and organic carbon from their food. In an ecological community, autotrophs also are called producers for their roles in the harness of solar energy to convert inorganic nutrients into energy rich organic material. Heterotrophs are called consumers, for their dependence on autotrophs for energy and nutrients.

Laws of Thermodynamics

The laws of thermodynamics set stringent constraints on the use of energy by every organism. It is important to know what these constraints are and their ecological implications. The first law of thermodynamics states that energy is conserved and can neither be created nor destroyed. During photosynthesis, the energy in light is used to convert carbon dioxide and water into glucose and oxygen. Part of the light energy is harvested by the plant and stored in glucose with the rest of the energy **dissipated**. The amount of energy involved in photosynthesis remains the same before and after the process. The amount of energy that can be conserved by the process, the chemical energy stored in glucose, however, is constrained by the second law of thermodynamics.

dissipate to reduce by spreading out or scattering

Any natural process that involves the use, transformation, and conservation of energy is constrained by the second law of thermodynamics. The law requires that any **irreversible** process will result in the degradation of the energy involved. In other words, there is an energetic cost associated with every irreversible process. Each organism is a complex biochemical machine that is made up of a network of metabolic pathways. Every metabolic pathway amounts to a nonequilibrium chemical reaction and therefore is an irreversible process. Using photosynthesis as an example, for every one hundred calories of light energy absorbed by a plant, the amount of energy that can be harvested and stored in glucose will have to be less than one hundred calories. The second law, however, does not provide guidance on how much of the energy will have to be degraded during each irreversible process. Direct measurement is needed to determine the actual efficiency.

irreversible unable to be reversed

The Structure of an Ecological Community

Energy flow in an ecological community must obey the laws of thermodynamics. These constraints affect the flow of energy and therefore the structure of an ecological community. Using the grazing food chain as an example, let's see how these laws affect the flow of energy at each trophic level. For the harvest of solar energy by plants in the production of plant tissues, the first law of thermodynamics requires that the amount of solar energy captured by the plants remain the same before and after the transformation; the energy involved cannot be created nor destroyed. For every thousand calories of solar energy captured and transformed by plant, there remain a thousand calories afterward. The second law of thermodynamics, however, requires that the harvesting of solar energy cannot be 100 percent efficient; only a portion of the solar energy transformed by the plant can be conserved in the production of plant tissue. Measurements on various plant communities show that the actual efficiency is below 10 percent. Most of the light energy, over 90 percent, is degraded by respiration into nonusable form. The rate of production of plant tissue, a reflection of the net harvesting of solar energy, is defined as the net primary productivity.

The transformation of energy at the second trophic level, or any other trophic levels, follows the same pattern. As a rule of thumb, 90 percent of the energy involved is degraded at each trophic transfer and only 10 percent of the energy is conserved in the organism's tissue. With 1,000 calories of solar energy captured by the plant, 100 calories of plant tissue can be produced, which in turn can be used to produce 10 calories of herbivore tissue, and in turn 1 calorie of carnivore tissue. The amount of energy potentially available to a species population is greatly influenced by its position on the food chain; the lower its position the more its available energy. This energetic constraint is widely reflected in many ecological communities, as herbivores, whether they are zebras or deer, usually outnumber their predators, lions or wolves. Because of this rapid decrease in the amount of usable energy, the length of the food chain is usually limited to a maximum of four to five levels. SEE ALSO Ecology; Ecology, History of; Odum, Eugene.

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Ecology, Fire

Fire has been an agent of change in nearly every terrestrial vegetation type on Earth, shaping both the species composition and structure. The probability of occurrence and the effects of fire vary widely depending upon the amount of fuel present, topography, climate, sources of ignition, and present species composition of the area. Fires may be severe, causing great mortality of existing plants and significantly changing the species composition

The California Department of Forestry holds a prescribed burn of shrub-chaparral mix in the Mojave Desert.

of the burned area, or they may have little impact on the composition and consume only the dry dead plant material present. They may burn intensely as fast-moving fires with flame lengths greater than 25 meters, or they may occur as slow-moving fires with flame lengths less than 0.5 meter. These sources of variation influence the effects that fire has on the vegetation and the ecological role of fire.

Prior to human intervention, fires occurred very frequently in some vegetation types. Fire history studies in temperate grasslands in Africa and North America, some ponderosa pine forests of western North America, and longleaf pine forests of southeastern North America indicate that fires occurred at an average of less than every ten years. When fires occur frequently, the vegetation's composition becomes dominated by fire-adapted (tolerant) species. Consequently, when fires occur, there is only minor change in species composition and the vegetation quickly recovers to the preburn condition, often within five years or less. The more frequently fire occurs on an area, the more it becomes dominated by fire-adapted species.

In other vegetation types, the fires may occur many decades or even centuries apart. Fires were naturally very infrequent in many arid areas where the fuels are not sufficient to carry a fire, or in humid areas where the fuels are seldom adequately dry to burn. Very often the effects of fire in these areas is long lasting and the vegetation may not recover for many centuries. When fires occur infrequently, fire-intolerant species become established, and the effects of fire are much more lasting. Even in these communities, however, fire may play important ecological roles in the functioning of the **ecosystem**.

ecosystem an ecological community together with its environment

Ecologists are becoming increasingly aware of the importance of fire in the maintenance and functioning of ecosystems. Rather than focusing on a single fire event, it is useful to apply the concept of a fire regime when considering the effects of fire on large areas over a long time. A fire regime describes the typical fire characteristics when applied to a landscape over many burning cycles. Fire regimes include characteristics such as frequency (how often the fire occurs over time), size, intensity (the rate at which fire consumes fuel and releases heat), severity (the effects of fire on the **biota** and soil), continuity (the degree to which unburned areas remain within the fire's perimeter), pattern (where fire typically occurs on the landscape), and variability in the previous characteristics. Modern humans have changed the fire regimes for many areas of the world. When fire regimes change, ecosystems and fire effects change in ways that are often not desirable. For instance, when fires are less frequent, they burn more intensely.

biota the sum total of living organisms in a region of a given size

Creation and Maintenance of Vegetation Composition and Diversity

Fire and other disturbances typically kill some plants and alter the competitive relationships between species. The initial postburn community is composed of those species that survive the fire and those that can efficiently migrate to the site. Community succession gradually modifies the postburn environment of the site and the composition changes in response to the changing environment. Species and, in some cases, the community may be replaced by later successional species and communities. Thus, fire plays a critical role in maintaining or creating new habitat for those species that are adapted to fire occurrence. For example, in many areas ponderosa pine-bunchgrass vegetation will gradually change to a forest dominated by other tree species, such as Douglas-fir, in the absence of fire. Periodic fires maintain the ponderosa pine-bunchgrass vegetation. A similar situation exists for many temperate grasslands, where in the absence of fire, grasslands are replaced through succession by forest or woodland vegetation.

In some instances, the vegetation itself must be removed by fire in order for the environment necessary for that vegetation to be maintained. For example, big sagebrush grassland often occurs in a fire-maintained mosaic with juniper woodland vegetation in western North America. In the absence of fire, the juniper woodland vegetation will replace the sagebrush grassland through community succession. Young juniper that are establishing within the sagebrush grassland can be readily killed by fire. Sagebrush will also be removed by the fire and a community composed of grasses and other herbaceous plants will become established initially. Sagebrush seedlings that cannot become established within a dense juniper woodland, however, will establish within the grassland and thus, over time, fire maintains the sagebrush grassland vegetation in the landscape.

Cycling of Organic Matter and Nutrients

In many areas of the world, the rates of plant **biomass** production exceed the rates of biomass decomposition. In these cold or dry areas, biomass tends to gradually increase over time as succession and plant growth

biomass the total dry weight of an organism or group of organisms

occur. Accumulation of biomass, particularly dead biomass, has many effects on the ecosystem. The nutrients essential to plant growth become increasingly concentrated in plant tissue and unavailable for subsequent plant growth. This may result in deficiencies of some essential nutrients and the reduction in biomass production. Fire rapidly cycles these nutrients and makes them available for future plant growth. In this way fire may help maintain the productivity of the ecosystem. The combustion process, however, results in the volatilization of some elements such as nitrogen and carbon, and these are lost to the atmosphere. Nitrogen is replaced in the ecosystem through nitrogen fixation and other processes of the nitrogen cycle.

Aboriginal Humans and Fire

In addition to its use for heating, lighting, and cooking, fire was the first tool that primitive peoples had to manipulate the environment on a broad scale to better meet their purposes. Fire has been used by hunter-gatherer societies to promote the production of certain wild crops (such as seeds: wild rice, sunflower, balsamroot, and mesquite beans; tubers: camas and bracken; berries: blueberry and blackberry; and nuts: acorns and chestnuts), increase the nutritional quality of forage for wild animals, create desirable habitat for game species, decrease the natural migration rates of game species allowing for increased hunting possibilities, control problem tick and insect populations, open travel corridors, and reduce fire hazard and enemy hiding cover in the vicinity of campsites.

Aboriginal people have also used fire for driving game species into traps or to hunters, long-distance signaling, warfare, and ceremonial purposes. Some peoples had the tradition of setting large fires in hopes that it would induce rain. **Pastoralists** used fire to clear pastures of trees and shrubs, increase forage production, improve forage nutritional quality, and decrease parasites affecting their livestock. Early agricultural cultures used fire to clear natural vegetation to facilitate **cultivation**, remove organic crop residue, and fertilize fields by cycling nutrients. In addition, many fires were likely set by accident from cooking fires. Thus, human culture has had a long association and evolution with fire.

pastoralists farming people who keep animal flocks

cultivation growth of crop plants, or turning the soil for this purpose

Use of Fire as a Land Management Tool

The intentional use of fire to achieve a land management objective is often referred to as prescribed burning. The fire is prescribed in the sense that the specific area, burning conditions, and expected results are identified prior to ignition. In addition, specific land management objectives are developed that justify the use of fire. Weather conditions (such as wind, temperature, relative humidity, and fuel moisture) and ignition patterns are selected that allow the land manager to control fire spread and achieve desirable effects on the vegetation. The management objectives of today's prescribed burning remain very similar to many of the aboriginal people's uses. The most common objectives include: creating or maintaining habitat for wild and domestic plants and animals, controlling undesirable plants, increasing the nutritional quality of forage for wild and domestic **herbivores**, reducing fire hazard through fuel reduction, and increasing nutrient cycling rates. Fire continues to be extensively used as a land treatment by hunter-

herbivore an organism that feeds on plant parts

gatherer, pastoral, and agricultural peoples around the world to clear vegetation, improve pastures, and remove crop residue.

Natural fire programs are employed in some national parks and wilderness areas to maintain the ecosystem in nonhuman-affected conditions as much as possible. Natural fires are those that have a nonhuman ignition source, primarily lightning. Prior to initiating a natural fire program, land managers develop a plan that identifies the conditions under which lightning-ignited fires will be allowed to burn without direct fire suppression control measures being taken. Since the weather conditions or location of any specific fire cannot be precisely predicted, however, the expected results of fire are usually described in more general terms than for human-ignited fire. The objectives of these fires usually includes having fire play a natural role in the ecological processes of the ecosystem. SEE ALSO CHAPARRAL; CONIFEROUS FORESTS; ECOLOGY; GRASSLANDS.

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Ecology, History of

Historians have debated the origins of ecology for decades. But there is no particular person or precise date or definite occurrence that marks the beginning of the science. Ecology gradually emerged as a distinct discipline during the latter part of the nineteenth century from a diverse array of different areas, including plant geography, plant **physiology**, taxonomy, and Charles Darwin's theory of evolution.

physiology the biochemical processes carried out by an organism

Linnaeus and Humboldt

One of the most important individuals in the early development of an ecological view of nature was Swedish botanist Carolus Linnaeus (1707–1778). Linnaeus was the father of modern taxonomy, the science of identifying and naming species. His great goal was to describe and catalog all known organisms. In 1749 Linnaeus published a book called *The Oeconomy of Nature*. In this book Linnaeus presented his view that nature, while seemingly chaotic and unpredictable, actually existed in a balanced state of order as designed by the creator. Linnaeus felt that if one looks closely at nature it is clear that even the simplest organisms have an important role to play in this natural economy; that no living thing is useless.

By the end of the eighteenth century, many scientists began to question Linnaeus's views. They felt that he had been far too descriptive in his approach to understanding nature. Rather than the static, harmonious world that Linnaeus envisioned, nature was dynamic and constantly changing. The chief proponent of these views was German explorer and scientist Alexander von Humboldt (1769–1859). Humboldt insisted that the only way to understand nature's complexity was to take accurate measurements in the field and then search for general laws. Influenced by German philosopher Immanuel Kant (1724–1804), von Humboldt believed that nothing in nature could be studied in isolation. All phenomena were connected.

Darwin and Haeckel

While some historians claim that von Humboldt single-handedly created the science of ecology, the true origins of modern ecology are found in English naturalist Charles Darwin's (1809–1882) *On the Origin of Species*, published in 1859. Darwin's theory of evolution by natural selection provided a mechanism, not only for understanding how species arose, but also for interpreting patterns in the distribution and abundance of species. A central insight of *Origin* was that plants and animals had the potential to reproduce very quickly and reach huge population densities. Darwin realized that this potential was rarely achieved because each species is subject to a series of natural checks and balances. "Look at a plant in the midst of its range," said Darwin, "Why does it not double in numbers? . . . To give the plant increasing numbers, we should have to give it some advantage over its competitors or the animals that prey upon it." While Darwin's work laid the foundation for the emergence of ecology thirty years later, there was no term that clearly defined the new area of biology that he had created.

The German biologist Ernst Haeckel (1834–1919) soon provided a name for the science that Darwin founded. Greatly influenced by Darwin, Haeckel published the *Morphology of Organisms* in 1866 with the aim of interpreting anatomy in the light of evolution. In this book, Haeckel provided the first definition of ecology: "By ecology we mean the body of knowledge concerning the economy of nature—the total relations of the animal to both to its inorganic and organic environment."

Thanks to Haeckel, ecology finally had a name. But for almost two decades no one seemed to notice. In the 1880s and 1890s, however, ecology experienced an explosion of interest. In Germany in 1885, Hans Reiter published the first book with the new term "oekology" in its title. In Denmark, the botanist Johannes Eugenius Warming (1841–1924) began to study plant physiology in relation to the environment and published the first textbook on plant ecology in 1895. In America, ecology gained almost instantaneous recognition amongst botanists and soon attracted a following of bright, young researchers. The first mention of Haeckel's term in the American press occurred on December 1, 1892, in the *Boston Globe*. A front-page article read "New Science. Mrs. Richards Names It Oekology." (Mrs. Richards was the leading conservationist of her day and the first director of the Water Quality Lab at the Massachusetts Institute of Technology.) In 1893 the first book in English with ecology in its title, *Flower Ecology* by L. H. Pammel, was published. Also in 1893, the Madison Botanical Congress adopted the term "ecology" as denoting a new branch of botany distinct from physiology and **morphology**.

morphology shape and form

The Twentieth Century

By the start of the twentieth century American plant ecologists had taken a leading role in the development of the new science. At the University of Chicago, Henry Chandler Cowles (1869–1939) began a series of classic studies on ecological succession in the dunes around Lake Michigan. At the University of Nebraska, Frederic Clements (1874–1945) developed new dynamic theories of plant associations and vegetational change. Other ecologists soon challenged the ideas of Cowles and Clements. The British ecologist Arthur Tansley (1871–1955) developed the concept of an ecosystem as an alternative to Clements's classification of plant communities. American botanist and plant ecologist Henry Allan Gleason (1882–1975) criticized Clements's idea of the plant community as a superorganism and proposed an alternative individualistic theory of plant associations.

holistic including all the parts or factors that relate to an object or idea

In the era following World War II, plant ecologists abandoned many of the central principles developed by Clements, including the idea of the stable climax association. They reexamined the central issue of community ecology: whether communities were simply chance associations of independent species or integrated, **holistic** entities that could not be understood by studying individual species. In the 1950s American botanist and ecologist Robert Whittaker (1920–1980) created a technique called gradient analysis that helped to resolve this question. Whittaker's pioneering studies indicated that plant species had unique and fairly independent distributions across physical gradients such as moisture and temperature. These studies led ecologists to reject Clements's theory of holistic plant communities composed of predictable associations of species that shared similar environmental constraints.

biotic involving or related to life

Under the influence of American ecologist and educator Eugene Odum (1913–), a whole new subdiscipline of ecosystems ecology grew to prominence during the latter half of the twentieth century. Ecosystems ecology emphasized both the **biotic** and physical aspects of the environment. In particular, ecosystems ecology was concerned with the large-scale flows of energy and nutrients through ecological communities. The International Biological Program, and studies by Gene Likens and E. Herbert Bormann of nutrient budgets in the Hubbard Brook Experimental Forest, helped to bring the ecosystem approach to plant ecology into the mainstream of ecological science. While ecosystems ecology has fostered new methods of understanding the complex dynamics of natural systems, it has remained largely separate from more traditional branches of ecology that emphasize populations and individual adaptations.

biodiversity degree of variety of life

In the 1990s plant ecologists became increasingly concerned with issues related to **biodiversity** and the loss of plant habitats due to human activities. Human beings have destroyed about half of the forests that once covered 40 percent of the planet. Each year over 150,000 km^2 of tropical rain forest are lost to logging, farming, and fire. At this rate there will be no rain forests left in fifty years or less. Earth's plant communities provide homes for millions of different species. They cleanse the air and water, protect against erosion, and replenish the soil. What are the ecological consequences of the continued destruction of forests and other plant habitats? How can what is left be preserved? These and other questions regarding the management and maintenance of the natural world will be the consuming issues for plant ecologists over the coming decade. SEE ALSO CLEMENTS, FRED-

ERIC; DARWIN, CHARLES; ECOLOGY; ECOLOGY, ENERGY FLOW; ECOLOGY, FIRE; HUMBOLDT, ALEXANDER VON; LINNAEUS, CAROLUS; ODUM, EUGENE; PLANT COMMUNITY PROCESSES; WARMING, JOHANNES.

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Economic Importance of Plants

Plants are extremely important in the lives of people throughout the world. People depend upon plants to satisfy such basic human needs as food, clothing, shelter, and health care. These needs are growing rapidly because of a growing world population, increasing incomes, and **urbanization**.

urbanization increase in size or number of cities

Plants provide food directly, of course, and also feed livestock that is then consumed itself. In addition, plants provide the raw materials for many types of pharmaceuticals, as well as tobacco, coffee, alcohol, and other drugs. The fiber industry depends heavily on the products of cotton, and the lumber products industry relies on wood from a wide variety of trees (wood fuel is used primarily in rural areas). Approximately 2.5 billion people in the world still rely on subsistence farming to satisfy their basic needs, while the rest are tied into increasingly complex production and distribution systems to provide food, fiber, fuel, and other plant-derived **commodities**. The capability of plants to satisfy these growing needs is not a new concern. The Reverend Thomas Malthus (1766–1834) in his *Essay on the Principle of Population* in 1798 argued that population growth would exceed nature's ability to provide subsistence. According to the U.S. Census Bureau, the world population was about one billion in 1800, doubled to two billion in 1930, doubled again to four billion in 1975, and reached six billion people in 2000. World population is expected to be nine billion by the year 2050. The challenge to satisfy human needs and wants still exists.

commodities goods that are traded, especially agricultural goods

Income has also been increasing rapidly throughout most of the world at the same time. U.S. census estimates are that the gross national product reached $27,000 per person in 1997 and is expected to reach $69,000 in 2050 assuming a 1.8 percent annual rate of growth. Income per person in many countries of Asia, Latin America, and Africa has increased more rapidly, but continues to be less than in other areas such as Western Europe and the United States. As income grows, plants become more valuable because people want to buy more and higher-quality products to satisfy basic needs.

Increasing urbanization leads to an increase in demand for marketing services as populations relocate from rural areas to urban areas. According to the Census Bureau, the U.S. population, for example, changed from 60 percent rural in 1900 to less than 25 percent rural in 2000. This urbanization demands more marketing services to assemble, sort, transport, store, and package large quantities of foods from production centers to consumption centers.

Value of Plants

According to the United Nations Food and Agriculture Organization, the estimated export value of major plant commodities traded in world markets for 1998 was: rice ($9.9 billion dollars), maize ($9.1 billion), wheat ($15.1 billion), soybeans ($9 billion), coffee greens and roast ($13.7 billion), sugar ($5.9 billion), tobacco ($24.1 billion), cigarettes ($15.4 billion), lint cotton ($8.2 billion), forest products ($123 billion), and forest pulp for paper ($13 billion).

Markets, a place where people buy and sell goods and services, determine the economic value of plants. The value depends on the expected uses and benefits provided. The economic value of plants is measured by their prices in a market economy. Demand and supply determine the price. In most countries, markets operate freely with little direct government interference in trading. In centrally planned economies such as China, however, the government frequently controls market operations, and buys and sells through government companies. In planned economies, governments may set prices administratively at levels that do not indicate true economic value to consumers and producers. As world economies become more open and market-oriented through trade agreements such as those that come from the World Trade Organization, the value of plants will likely become more equal among countries.

Two main types of markets set the value of plants: cash markets and future markets. The most common type is a cash market. Cash markets are very popular places throughout the world where buyers and sellers meet to exchange money for goods and services. Demand and supply in the cash market set the price at which buyers will exchange money with sellers for immediate possession of goods. In the simplest case, producers take goods to the market for immediate sale, and consumers arrive with cash to buy goods for immediate possession. In more complex cases, producers sell goods to one or more other buyers who in turn sell the goods to consumers.

Cash markets operate daily, weekly, or for other intervals all over the world. Consumers and producers trade in thousands of cash markets operating in the world today. These local cash markets in rural areas are linked to larger regional trading centers that in turn are linked to cash markets in the larger cities. Cash markets operate for all the major plant products.

Futures markets, a second major market to set the economic value of plants, operate very differently from cash markets. In cash markets buyers and sellers trade the physical good, whereas in futures markets buyers and sellers trade a futures contract. Futures contracts are standardized written documents calling for future delivery of a good at a particular time and place in the month of expiration. Futures markets attempt to discover the best value today for a good tomorrow based upon expected demand and supply in some future time period.

Futures markets have become increasingly popular around the world. Important futures exchanges include the Chicago Board of Trade for grains and oilseeds; the Chicago Mercantile Exchange for livestock, dairy products, and lumber; and the New York exchanges for cocoa, coffee, cotton, orange juice, and sugar. Futures contracts are traded on exchanges in Great

Britain, France, Japan, Australia, Singapore, and Canada. In addition, Brazil, China, Mexico, Italy, and Spain (to name a few) have futures exchanges.

It is interesting to note that futures markets do not trade contracts in fruits and vegetables and other highly perishable products. Futures trading is not possible for highly perishable products because of the difficulty of long-term storage.

Marketing Systems for Plants

The marketing system for most plants can be viewed as an hourglass shape that concentrates production from many farms into large quantities and fewer firms for processing and handling, followed by a distribution into smaller quantities and more firms for sale to many consumers. Marketing systems add value as the plants progress from the farmer to the consumer. The added value takes the form of marketing services that transform a raw commodity into a finished product for consumer use. Depending on the commodity, these services include cleaning, sorting, grading, packaging, storing, transporting, handling, processing, and financing until goods are sold to the consumer.

Farmers usually sell their goods at harvest time in local markets to buyers who may come from large urban or smaller regional trading centers, or farmers sell to agents of those buyers. The buyers assume the risks of ownership until they are able to sell the goods to consumers at a later time. The ownership risks include providing many valuable marketing services to assure that products will be available in the right quality, in the right place, at the right time, in the appropriate amount, and for a reasonable price.

The difference between the value paid by consumers for plants and the value received by producers is the marketing margin, which is the amount charged by the businesses for the services provided. For example, if the consumer pays one dollar for a product in the supermarket, and the producer receives forty cents, then the marketing margin is sixty cents.

Higher incomes and growing populations mean that consumers will demand more marketing services that increase convenience and reduce preparation time, such as slicing, freezing, packaging, and ready for microwaving. In addition, as per capita income increases, the composition of demand for food changes to increased consumption of higher-value products. These changes typically mean increased consumption of products such as fruits and vegetables, meat, dairy, and processed products, and decreased consumption of staples such as potatoes, cassava, and rice. More marketing services are required for high-valued products.

As consumers demand more marketing services, the marketing margin will increase, causing the farmers' share of the consumer food dollar to decline. In many countries, the farmers' share of consumer expenditures (about 40 to 50 percent) is already declining, as marketing margins increase. John Abbott in *Agricultural and Food Marketing in Developing Countries* indicated that margins also vary by country for the same commodity due to differences in income, geography, **infrastructure**, and marketing systems.

infrastructure roads, phone lines, and other utilities that allow commerce

The farmers' share of consumer food expenditures has declined steadily through time in the United States to about 21 percent in 1993; ranging from

25 percent for food consumed at home to 15 percent for away-from-home consumption. This declining farmers' share can be expected to continue as income increases. A declining farmers' share does not mean that the marketing system is inefficient or that farming is unprofitable. Technical progress that increases productivity generally will result in declining real prices per unit of output.

Farmers can increase their share of the consumer food expenditures by adding value to what they sell. Some examples of added value are direct sales to consumers at farmers' markets, roadside markets, and farmer-owned marketing and processing cooperatives. Paul Eck in *The American Cranberry* described Ocean Spray cranberry juice as a most successful story of farmers adding value to cranberries. Cranberry growers formed a cooperative to process and market Ocean Spray cranberry juice more profitably, a product that has great brand identification with consumers. SEE ALSO AGRICULTURE, HISTORY OF; AGRICULTURE, MODERN; ALCOHOLIC BEVERAGE INDUSTRY; ALCOHOLIC BEVERAGES; ALLIACEAE; CACAO; COFFEE; CORN; COTTON; FIBER AND FIBER PRODUCTS; FORESTRY; FRUITS; GRAINS; OILS, PLANT-DERIVED; PAPER; POTATO; POTATO BLIGHT; RICE; SUGAR; TEA; TOBACCO; VEGETABLES; WHEAT.

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Ecosystems

Systems are assemblages of interacting objects that are linked by transfers of energy and matter, behave in specific ways under certain conditions, and are often governed by cybernetic controls that involve the flow of information through positive and **negative feedback**. In 1935 British ecologist Arthur Tansley (1871–1955) described functioning organisms and their physical environment as the "basic units of nature on the face of the Earth" and referred to them by the term "ecosystem." The components are both living (within the biotic realm) and nonliving (abiotic). The biotic components comprise the communities of organisms formed by interacting populations. While ecosystems are real, functioning places, they are also the abstractions, or models, that are developed to characterize the function and potentially predict the behavior of these real places.

negative feedback a process in which a change in some variable leads to a system response that minimizes that change

One important aspect of ecosystems is the definition of their boundaries. In some cases this is superficially obvious. A pond can be thought of as an ecosystem with the boundaries between the water and the terrestrial

Interior of Biosphere II, an enclosed ecosystem, at Oracle, Arizona.

environment forming a shoreline, the interface between the water surface and the atmosphere defining the top, and the lower extent of wet sediments in the ooze at its bottom as recognizable surfaces. Even these, however, are not quite as clear-cut as they may seem when viewed in closer detail. The shoreline is much longer when measured with centimeter segments than with a meter stick. The water surface boundary has a layer of air **saturated** by water vapor that may or may not be considered to be part of the ecosystem; and the bottom could be complicated by the presence of the inlet from an underground spring. Boundaries are even harder to define within an expanse of seemingly continuous grassland or forest, and are therefore at times assigned in an arbitrary manner by researchers.

saturated containing as much dissolved substance as possible

Size alone does not necessarily help resolve the question. In some cases the interactions within an ecosystem occur over many kilometers, and the boundaries are formed by decreasing probabilities of transfers of matter and energy with other parts of the system. On the other hand, sometimes very small units can be thought of as ecosystems. The moss-covered back of a sloth, a pile of bear dung, or the surface of your skin can be treated theoretically as a microcosm or miniature ecosystem. The frequent indistinctness of boundaries, and the fact that energy and matter enters and leaves the ecosystem, makes them open systems. Even if energy gains and losses are in balance, it is more appropriate to describe an ecosystem as a steady state rather than equilibrium, because equilibrium (which is only possible in a completely isolated, thermodynamically closed system), does not adequately model ecosystems. They are always dynamically interacting with adjacent ecosystems to form a complex landscape.

One of the most powerful tools emerging from the ecosystem concept is the development of models that abstract the structure and function of the real world. Pictures and graphs describe physical arrangement of objects. Flow charts characterize highly probable pathways for energy or nutrients to pass through the system. In the case of energy, this flow is a one-way street with its ultimate dissipation outside of the boundaries as heat and entropy. Nutrients, however, can be retained and recycled within the ecosystem. The extent to which this happens is one measure of stability.

The beauty of ecosystem models is that they can be quantified. This allows them to be analyzed mathematically on computers and ultimately, if the models are based on real, natural behaviors, they can be used to predict the future of ecosystems. The rapidly developing field of general systems theory can be applied to ecosystems resulting in insights about how they function. These tools also allow ecologists to make predictions about the behavior of ecosystems when disturbed, stressed, or altered by evolutionary time, questions that society is finding pressing with increasing pollution, global warming, and other environmental threats. SEE ALSO Agricultural Ecosystems; Aquatic Ecosystems; Biome; Coastal Ecosystems; Ecology, Energy Flow; Ecology, Fire; Ecology, History of; Plant Community Processes.

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Embryogenesis

The development of the embryo, or embryogenesis, begins with the repeated divisions of the **zygote** to give rise to thousands of cells. These in turn form the various tissues and organs of the adult plant. In seed plants, embryogenesis occurs within the embryo sac of the ovule. Since the ovule is transformed into the seed, embryo development is intimately associated with seed formation.

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

Dicot and Monocot Embryos

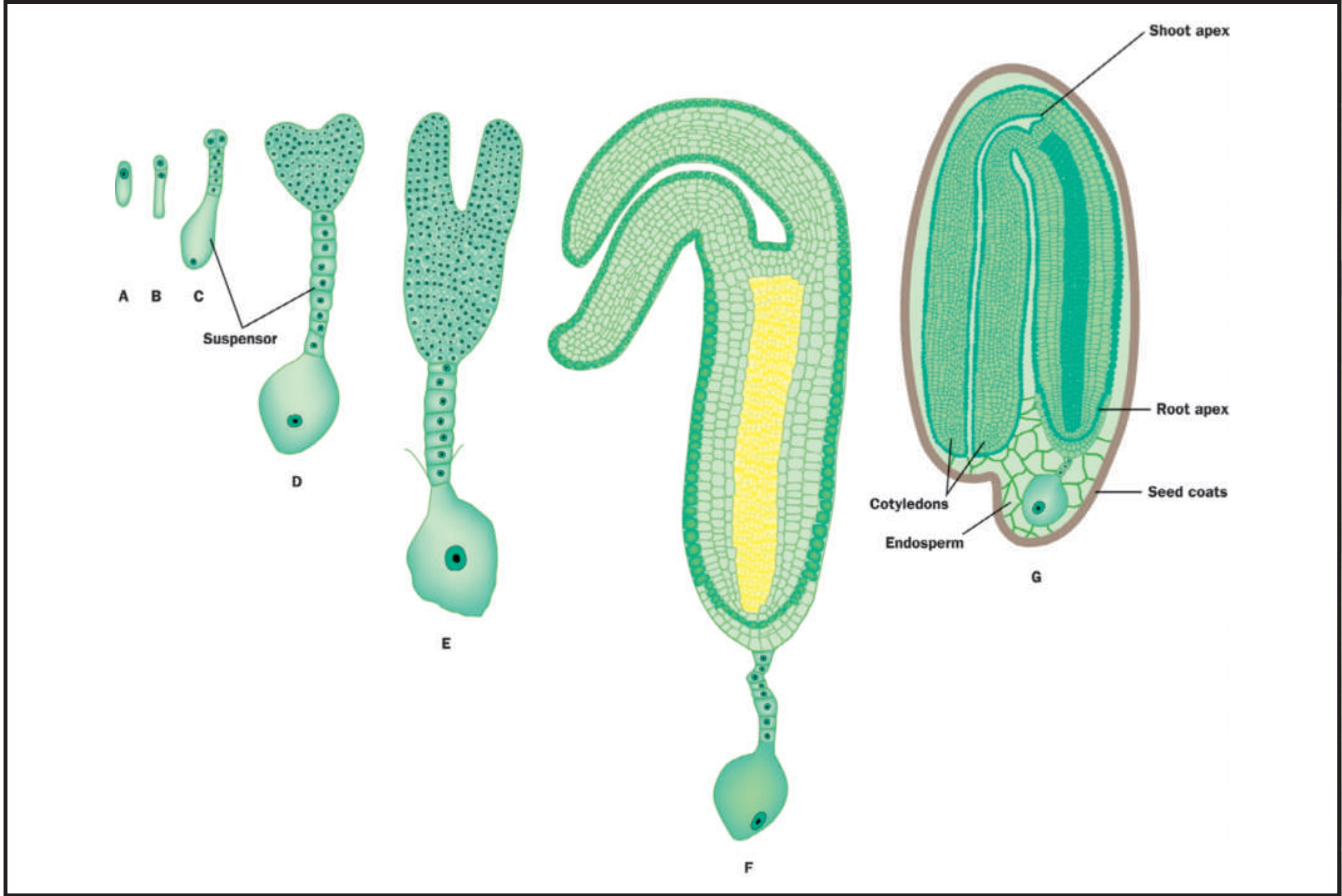
The first division of the zygote is almost always asymmetric (uneven) and **transverse to** its long axis, producing a small **apical** cell and a large basal (bottom) cell. The apical cell then divides, forming a longitudinal wall, and then divides again, forming a second wall at right angles to the first, to generate a four-celled embryo; subsequent divisions give rise to a globular embryo of eight to thirty-two cells. By changes in shape, accompanied by tissue and organ formation, the globular embryo successively forms the heart-shaped, torpedo-shaped, walking-stick-shaped, and mature embryo.

transverse to across, or side to side

apical at the tip

In contrast, the basal cell divides by a series of transverse walls to form a **filamentous** structure known as the suspensor, which anchors the embryo to the embryo sac wall and aids in nutrient absorption from the

filamentous thin and long



Diagrammatic representations of embryogenesis and seed formation in *Capsella bursa-pastoris.* A) Zygote. B) First zygote division producing a small apical cell and a large basal cell. C) Further divisions of the apical cells and basal cells to form the globular embryo and suspensor, respectively. D) A heart-shaped embryo. E) A torpedo-shaped embryo. The suspensor has attained its maximum development. F) A walking-stick-shaped embryo. Suspensor degeneration begins. G) A mature embryo enclosed inside the seed and covered by seed coats. Only a few endosperm cells are present; suspensor loses its connection with the embryo.

surrounding tissues. Typically in dicots, the mature embryo consists of the shoot apex, the two cotyledons (seed leaves), the hypocotyl (primitive stem), and the root. Together, these occupy most of the volume of the mature seed. Although the early division sequences of embryos of monocots appear somewhat similar to those of dicots, several organs not found in dicot embryos assume prominence in monocot embryos, especially in embryos of cereal grains. In the latter, the single cotyledon (known as the scutellum) functions to absorb nutrients from the endosperm. Sheathlike structures, known as the coleorhiza and coleoptile, cover the root and shoot, respectively. Finally, a flaplike outgrowth called the epiblast is found at the origin of the coleorhiza. The mature embryo is confined to a small part of the cereal grain, which is filled with the nutritive tissue of the endosperm.

Tissue Formation in the Early Embryo

Although embryos lack most organs of the adult plant, the characteristic body plan of the adult is nonetheless established during early embryogenesis. This involves the formation of an apico-basal (top-bottom) axis, constituting the body of the embryo, and a radial axis of differentiated tissues around the apico-basal axis. In dicots, the apico-basal axis is established as early as the four-celled stage of the embryo, when a transverse division gives rise to upper and lower tiers of four cells each. The shoot apical meristem and cotyledons are generated from the upper tier of cells, and the

Genetic and molecular studies of embryogenesis in *Arabidopsis thaliana* have shown that specific genes control the formation of both apico-basal and radial pattern elements in the embryo. Among the genes isolated and characterized are *Gnom*, *Monopteros*, and *Shoot Meristemless*, controlling the apico-basal pattern, and *Knolle*, controlling the radial pattern.

meristem the growing tip of a plant

epidermis outer layer of cells

primordial primitive or early

vascular related to transport of nutrients

lateral away from the center

hypocotyl and root are generated from the lower tier. Thus, the primary **meristems** of the shoot and root come to occupy positions at opposite poles of the embryo axis. In *Arabidopsis thaliana* and *Capsella bursa-pastoris*, two model species to study embryogenesis in dicots, the uppermost cell of the suspensor (known as the hypophysis) functions as the founder cell that generates parts of the embryonic root such as the root cap, cortex, quiescent center, and **epidermis**.

After the apico-basal axis is established, the radial pattern elements of the **primordial** tissue layers are laid down in the eight-celled embryo by a new round of divisions. These create an outer layer of eight cells (forming the protoderm) and an inner core of eight cells (forming the ground meristem and procambium). The protoderm and procambium become the epidermal and **vascular** tissues, respectively, of the mature embryo, whereas the cells of the ground meristem differentiate into a cortex or into both cortex and pith. In cereals such as maize, the globular embryo of sixteen to thirty-two cells attains a club-shaped stage when the scutellum appears as a vague elevation at the apico-basal region. The shoot apex and leaf primordia are formed as **lateral** outgrowths opposite the scutellum. Finally, the appearance of the coleorhiza and the differentiation of the root in the central zone of the embryo complete the process of embryogenesis. In both dicot and monocot embryos, the active life of the suspensor is terminated when the embryonic organs are formed. SEE ALSO CELLS, SPECIALIZED TYPES; DIFFERENTIATION AND DEVELOPMENT; GENETIC MECHANISMS AND DEVELOPMENT; GERMINATION; REPRODUCTION, FERTILIZATION AND; SEEDS; TISSUES.

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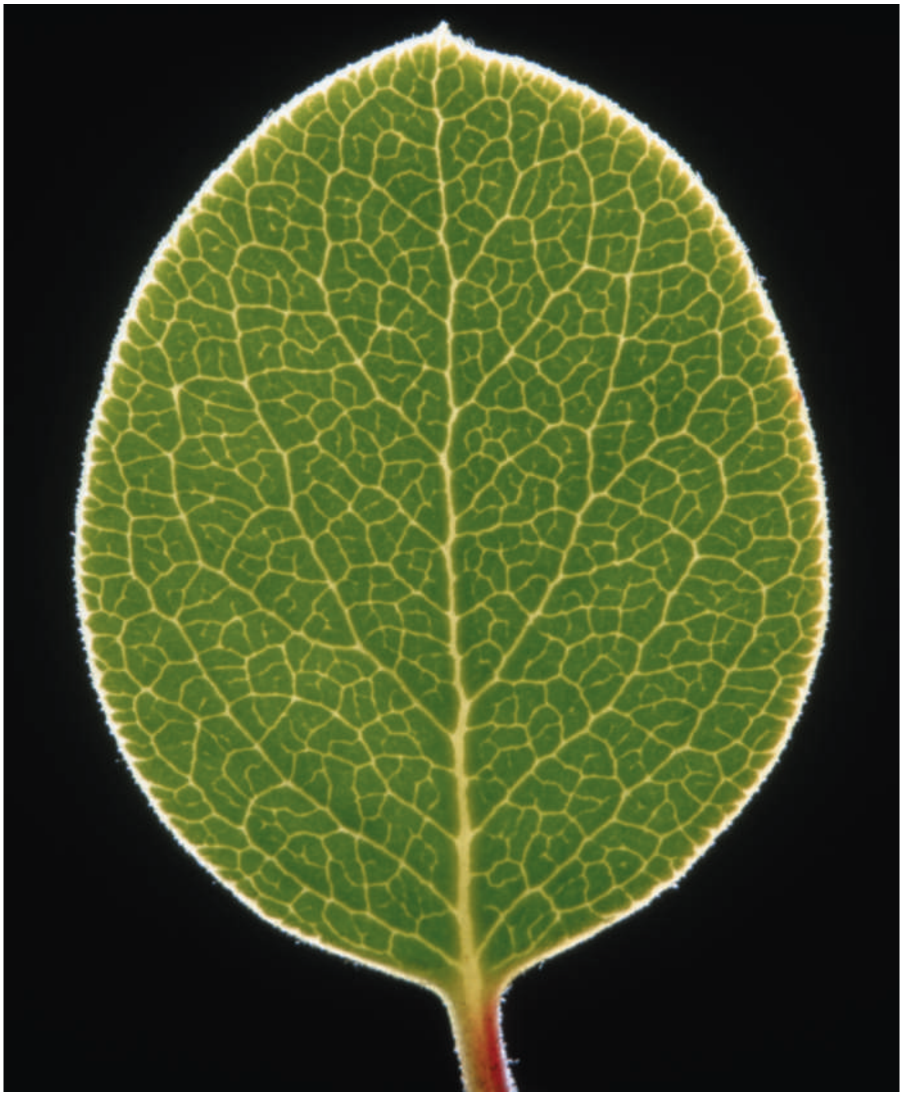
Endangered Species

An endangered species is a species that is in immediate danger of becoming extinct. The designation of *endangered* to a species means that there is still time to save it but once it is extinct it is gone forever. Also of concern are threatened species, species whose numbers are low or declining but not in immediate danger of extinction. A *threatened* species is likely to become endangered if it is not protected.

Most species that are endangered are found in only limited geographic areas. Because these plants or animals are not widespread to begin with, they are more likely to be affected by major or catastrophic changes in their environment. Widespread common species, while sometimes significantly hurt by a regional catastrophe, are more likely to survive because many individuals will escape the damage elsewhere. In contrast, species found only in small and unusual habitats can suddenly become endangered or extinct if their limited habitat disappears.



A leaf of the Presidio manzanita in San Francisco's Golden Gate Park. Only one such plant survives in the wild.

Processes That Threaten Endangered Species

Extinction can be part of the natural order. Only about one in a thousand of all of the species that have ever lived on Earth is still living today. The vast majority became extinct because of naturally changing physical and biological conditions. Changing climate such as that experienced during the Ice Age (which eliminated many plant species from very large areas of North America and Europe) and other natural events such as volcanic activity have caused localized plant extinctions. The slow movement of the continents (most notably Antarctica and Australia) into unsuitable climate zones caused many organisms to become extinct. Far more widespread and devastating natural extinctions have been caused by the rare impacts of asteroids and comets on the Earth. Some impacts have caused the extinction of even common species on a global scale.

The danger to plants and animals today is most often a direct result of human activities and human population increase. These activities have taken the form of habitat alteration, economic exploitation, the intentional elim-

The Beni Biosphere Reserve in Bolivia. Managing ecosystems or saving species collectively is the best known solution for protecting endangered species.

ination of pests, the introduction of exotic (nonnative) organisms, the increase of invasive native grazers, and the effects of environmental pollution.

Habitat alteration is the main factor endangering species throughout the world, from the American Midwest where the prairies have been converted to cropland to the equator where the tropical rain forests are being cut and burned. Wetlands filling and draining, agricultural expansion, and residential housing development are all significant factors in habitat destruction.

Trade in live plants and animals and the products made from them is the second greatest factor endangering species. The cutting of forests for wood and fuel, the digging of rare plants for sale, and the harvesting of medicinal plants for commerce is as common as the illegal hunting and poaching of animals for sport, food, products, or pets. Plant examples include such species as ginseng, which has been harvested in several states to the point of near extinction.

The intentional elimination of species is a third human factor endangering species. Many plants and animals have become endangered or extinct simply because people decided they were pests. Killing for the sake of eliminating an unwanted animal or plant has been common, as seen in the burning or clearing of forests for agriculture or other development, or in the killing of lions, wolves, sharks, or many snakes considered to be pests.

Invasions by exotic species (animal or plant species that have been introduced to an area where they did not naturally occur) threaten many endangered plants. When plants or animals are introduced into an area where they have no natural enemies, they may start to compete with the native plants and animals for food, water, shelter, and space and often replace them. Some plant examples include teasel and aggressive European pasture grasses that have invaded the few remaining tallgrass prairies or aquatic plants that have clogged streams and canals. The introduction of goats to tropical islands, for example, has caused the endangerment and extinction of many plant species that were not adapted to such grazing. A similar impact to plants can occur from locally overabundant or expanding native species such as beavers, rabbits, and deer that have altered many habitats because of the elimination of their former natural predators. For example, in many areas of the midwestern and eastern United States, heavy browsing by white-tailed deer is preventing the regeneration of the endangered components of native plant communities. Conservation biologists must be as effective in controlling invasive and destructive species as they are at saving endangered native species.

Environmental poisons and pollution are endangering numerous plants and animals worldwide as well. Examples of plants and animals today that are being poisoned by environmental **toxins** and solid wastes such as deadly chemicals, oils, and acids are numerous. Scientists learned long ago that groups of organisms in a limited environment can be killed by their own wastes.

toxin a poisonous substance

Many Plants Are Endangered

One in ten, or a total of about three thousand plants native to the United States is endangered. Many of these endangered plants include some of the most showy, such as the large-flowered orchids. Increasingly, many plants around the world no longer reseed and therefore remain as lone survivors of their species. For example, the Presidio manzanita is so rare that only one plant survives in the wild, at San Francisco's Golden Gate Park. While cuttings have been **propagated**, they cannot self-fertilize. Another example of a lone survivor can be found on the Indian Ocean's Mascarene Islands where a palm tree, the *Hyophorbe amaricaulis*, survives as a single individual. One severe storm could cause its extinction. More than two hundred other plant species have also stopped reproducing. Worldwide, an impressive one in eight plants is endangered, according to the *1997 IUCN Red List of Threatened Plants*.

propagate to create more of through sexual or asexual reproduction

Plant Extinctions Are Increasing

Although conservation efforts have begun in recent years, people are still exterminating entire species at an ever-increasing rate. Since the Pilgrims landed at Plymouth Rock, more than five hundred species, subspecies, and varieties of our nation's plants and animals have become lost forever. By contrast, during the three thousand years of the Pleistocene Ice Age, all of North America lost only about ninety species. The situation is even worse in many other parts of the world. Some scientists believe that if present trends continue, two-thirds of the world's three hundred thousand plant species will disappear by the end of the twenty-first century.

Extinction is a difficult concept to fully grasp. We are very aware that dinosaurs no longer exist and that other animals (such as the mammoth, dodo, Carolina parakeet, passenger pigeon, and the Atlantic grey whale) are gone forever due to human activity. The Sexton Mountain mariposa lily, a flower of southwestern Oregon, was unintentionally exterminated by a road crew when Interstate 5 was built in the 1960s. The maidenhair (ginkgo) tree was planted by the Chinese in gardens many centuries ago before it became extinct in the wild. A few plants that have become extinct in the wild in recent times have been saved in some form in **cultivation**. The Franklin tree (*Franklinia*, named after Ben Franklin) was last seen in the wild in 1803 in Georgia. However, a few individuals were planted in gardens at that time and have been propagated, saving the species from total extinction. In the mid-1990s the Graves's beach plum, a seashore tree found only in Connecticut, became extinct in the wild when the only known individual died. A few cuttings have been saved in botanical gardens. Although cloning results in plants that are genetically identical, those that have become extinct in the wild but that have been saved in cultivation cannot effectively reproduce.

cultivation plant growth involving human intervention

Mechanisms of Environmental Protection for Endangered Species

Enacted in 1973, the Endangered Species Act (ESA) is the principal tool in the United States for slowing or stopping what has become the greatest rate of extinction worldwide since the disappearance of the dinosaurs sixty-five million years ago. In adopting the Endangered Species Act, Congress found that "various species have been rendered extinct as a consequence of economic growth and development untempered by adequate concern and conservation." In addition, Congress recognized that threatened and endangered species "are of aesthetic, ecological, educational, historical, recreational, and scientific value to the Nation and its people." Congress enacted the ESA in order "to provide a means whereby the **ecosystems** upon which endangered species and threatened species depend may be conserved" and to provide a program for the conservation of the species themselves. Under the ESA, species are listed as endangered or threatened. The Interior Secretary is generally required to designate critical habitats (areas essential to the survival and recovery of a species) for threatened and endangered species. In addition, recovery plans (blueprints for bringing species back to a point where they are no longer threatened or endangered) must be developed and implemented. About one-third of listed species are now stable or improving as a result of the ESA Protections for Listed Species. Effective protection is limited by the degree of funding and enforcement of the law.

ecosystem an ecological community together with its environment

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), convened in Washington, D.C., in 1973, has been signed by more than 120 countries. CITES was established for the purposes of controlling and monitoring international trade in plants and animals considered to be threatened or likely to be threatened through commercial exploitation. It states that flora and fauna comprise an "irreplaceable part of natural systems which must be protected for generations to come" and "international cooperation is essential for the protection of certain species . . . [endangered by] over-exploitation through international trade." This treaty was one of the first to take account of the need for conservation of both plants and animals and provided the legal framework within which those in trade can be protected from extinction.

Conservation practices provide the only solution for protecting endangered species. Propagation centers, such as botanical gardens, are actively attempting to save some endangered plant species. Protected collections of seeds and plants can help stop species loss, but protection in the wild is much more desirable because propagating endangered species can be considered to be meaningless if they do not have a home. Managing ecosystems or saving species collectively is the best known solution. Around the world more than thirty-five hundred protected areas (with a total of about 2 million square miles [5 million square kilometers], or 3 percent of Earth's land area) exist in the form of parks, wildlife refuges, and other reserves. Three percent of the planet's area, however, can only protect a relatively small number of species. SEE ALSO BIODIVERSITY; BOTANICAL GARDENS; GINKGO; INVASIVE SPECIES; RAIN FORESTS; SEED PRESERVATION.

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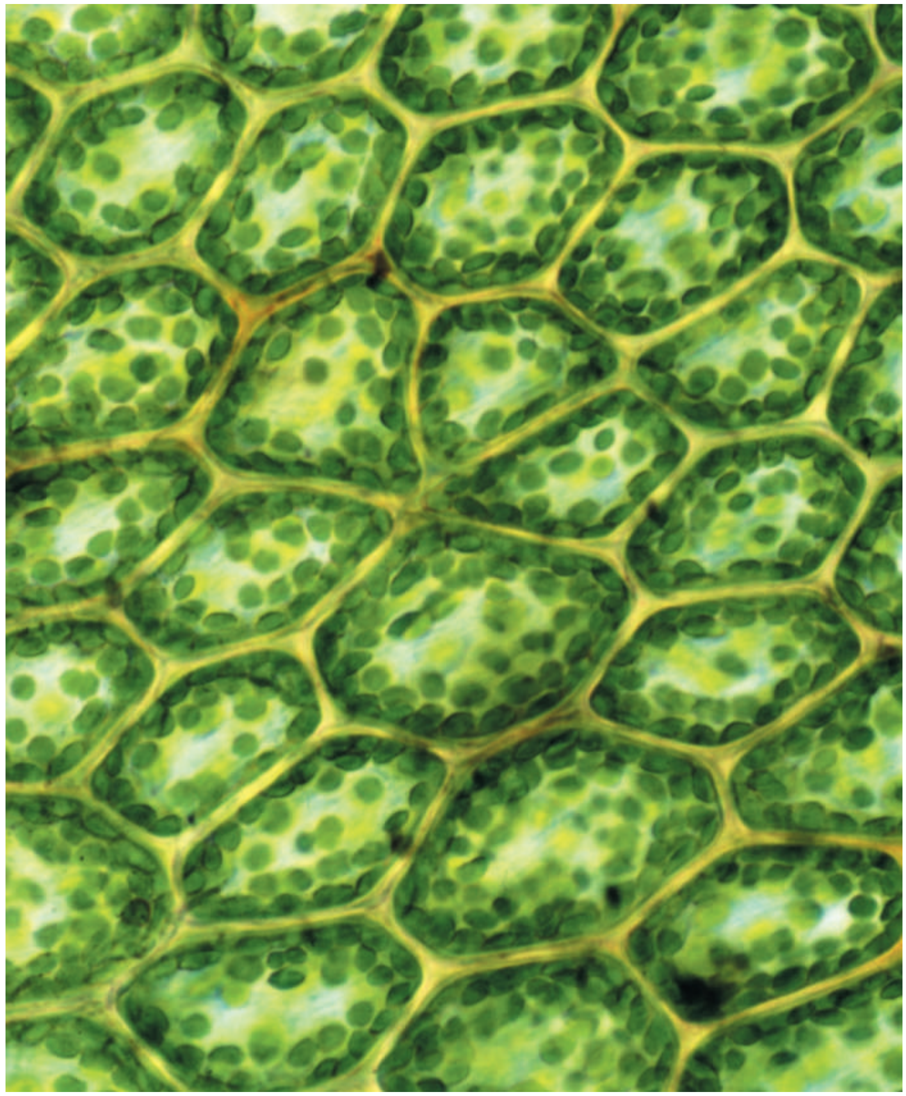
Endosymbiosis

Once considered a relative rarity, endosymbiosis, the living together of one organism inside another, has increasingly become recognized as a major factor in the evolution of life forms. The word *endosymbiosis* comes from Greek words meaning "inside," "with," and "living." Endosymbiosis in biology is a subdivision of the more general concept, symbiosis, which refers to living beings of different species living together for most of the life history of a member of at least one of those species. (In the case of the bacteria it suffices to say "living together of different types" because bacteria often cannot clearly be assigned to species.) Ectosymbiosis is a more familiar notion, A micrograph of a leaf, showing chloroplasts (green). These plastids are believed to have once been free-living photosynthetic bacteria that became parts of plant cells by endosymbiosis.



an association between organisms of different species where one is attached in some way to the outside of the other. Barnacles adhere to the hairy, wet surfaces of whales where the pattern of barnacle distribution is used by whales to distinguish each other. This is one example of ectosymbiosis.

Endosymbiosis often takes symbiosis proper a step further. As in sexual reproduction, genes from two beings come together giving added abilities to the mutual organism. Unlike in sex, however, the two organisms do not necessarily come apart immediately after their fusion. They may dwell in the same body forever. Indeed, permanent symbiosis has been proven as a means of producing new organisms.

The most stunning and momentous example of endosymbiosis is perhaps that of the photosynthetic parts of algal and plant cells, called plastids, which are now believed to have once been free-living photosynthetic bacteria. Red plastids of red algae are called rhodoplasts. The more familiar green plastids are called **chloroplasts**. The plastids that give plants and algae their metabolic ability to use light to produce chemical food and energy are the same size, shape, and composition as photosynthetic bacteria. They

chloroplast the photosynthetic organelle of plants and algae

also divide to reproduce by a process of fission—distinct from the complex mitotic division found in all nonbacterial cells with nuclei, such as plant, algae, and fungal cells. Genetic similarities in long stretches of deoxyribonucleic acid (DNA) show definitively that rhodoplasts are very closely related to cyanobacteria (oxygen-producing, green-tinged bacteria). Therefore, the direct link between cyanobacteria and the plastids of algae and plants is one of ancestry. Free-living cyanobacteria merged with nonphotosynthetic ancestors of the algal cell, including the algae that evolved into plants. Ancestors of plant cells, in other words, acquired their plastids, once free-living cyanobacteria, by endosymbiosis.

Plastids are one of a class of membrane-bounded cell structures called organelles. Others include mitochondria, bodies that react with oxygen to produce energy for the rest of the cell in which they reside. Mitochondria also contain their own DNA and are thought to be the descendants of formerly free-living bacteria. The details of how plastids, mitochondria, and other organelles came to live in permanent endosymbiosis with cells are complicated. The original union leading to the origin of plastids, however, is easy to envision. Some hungry, translucent **protists** ate delicious photosynthetic cyanobacteria and failed to digest them. In the light the cyanobacteria could not help but continue its photosynthesis. Hence, the merger, now a green cell, evolved from its cyanobacterial and **translucent** ancestors. With the passage of time the association became permanent, and resulted in the evolution of algae. Genes between the two types of life were exchanged. Eventually plants evolved from the endosymbiotic union. SEE ALSO Algae; Chloroplasts; Cyanobacteria; Eubacteria; Evolution of Plants; Plastids.

protist usually a single-celled organism with a cell nucleus, of the kingdom Protista

translucent allowing the passage of light

Lynn Margulis and Dorion Sagan

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Epiphytes

Epiphytes (*epi*, meaning "surface," and *phytes*, meaning "plants") are plants that live on host plants, usually in the treetops. They include a wide variety of growth forms, ranging from woody structures to herbs. Epiphytes are not parasites but simply rely on their host trees for support. In return, they collect enough light to manufacture energy and also provide food and shelter for many organisms living in the treetops, such as insects, birds, and other small animals. More than twenty-five species of epiphytes have been classified by botanists, and more are found each year as botanists continue to find new ways to climb into the treetops of the tallest, unexplored regions of tropical rain forests.

Epiphytes have unique ecological characteristics that enable them to survive in the forest canopy. Some of these special adaptations include:

- holdfasts or other ways of adhering to the bark or branches of trees, so that wind or other forces do not knock them down and so they can compete for sunlight in the canopy; epiphytes do not have conventional roots that extend into the soil

An epiphytic orchid on a tree trunk in Thailand.

herbivore an organism that feeds on plant parts

- evergreen foliage that is resistant to drying out in the hot, dry canopy and that is too tough to be chewed by insect **herbivores**
- plant shapes (e.g., cups or rosettes) that allow the collection of water, fallen leaves, and decomposing bodies of insects that together form a nutrient pool for the plant as well as for their aquatic animal inhabitants
- tiny seeds that are wind-dispersed and can lodge in tiny crevices in tree bark
- pollinators such as bees and flies that inhabit the canopy
- relationships with fungi (mycorrhizae) that aid the epiphyte in gathering additional nutrition for photosynthesis.

More than eighty families of plants contain species that are epiphytes, but only several have a significant number of species that are epiphytic in their habit. These include orchids (family Orchidaceae), bromeliads (family Bromeliaceae), cacti (family Cactaceae), ferns (family Pteridophyta), aroids (family Araceae), and several groups of ferns, mosses, and liverworts. Over twenty-five thousand species of epiphytes exist, including approximately twenty-one thousand orchids and over one thousand species of bromeliads.

Many animals depend on epiphytes for their existence in the canopy. Tarantulas often live within the rosettes of bromeliads, while bats, birds, and insects serve as important pollinator groups for bromeliads; lizards and birds visit epiphytes for feeding and drinking; insects dominate as pollinators of orchids; and ant-nest garden epiphytes provide nesting cavities and shelter for their ant residents. Tank epiphytes, those plants that contain a pool of water formed by tightly pressed leaves in a rosette, provide a mini-aquatic ecosystem in the canopy that has been shown to support over fifty species of animals, including mosquito larvae, tadpoles, beetles, spiders, flies, and even lizards. Because epiphytes are plants and produce their own energy, they actually provide nutrients to other organisms and thereby enhance the diversity of life in the forest canopy.

Relatively little is known about epiphytes in contrast to the plants' terrestrial counterparts because of their location high above the forest floor. During the past decade, new methods for reaching the treetops have been developed that provide better access for the study of epiphytes. These techniques include the construction of canopy walkways, the use of ropes and technical climbing hardware, hot air balloons and inflatable canopy rafts, and even construction cranes. The challenge of reaching epiphytes and their inhabitants has been overcome, and in the future more information will be discovered about these unique plants that inhabit the treetops. SEE ALSO Interactions, Plant-Plant; Mycorrhizae; Orchidaceae; Rain Forest Canopy; Rain Forests; Symbiosis; Trees.

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Ethnobotany

Ethnobotany is generally defined as the scientific study of the relationships between plants and people. The fungi, while comprising a kingdom of life completely separate from plants, and, according to molecular evidence, are more closely related to animals than plants, have in practice been included within the scope of ethnobotanical research, although the term *ethnomycology* is sometimes employed to refer to the relationships between fungi and people. Additional terms are sometimes used to distinguish other subdisciplines of ethnobotany, such as *ethnopteridology* (the study of relationships between people and ferns and related plants), but for purposes of this encyclopedia, all such subdivisions are considered to be within the scope of ethnobotany. Sometimes a distinction is made between the term *economic botany*, referring to the study of the use of plants by industrialized society, and *ethnobotany*, referring to the study of plants used by nonindustrialized cultures, but this distinction is increasingly blurring. Sometimes economic botany is considered to be the broader discipline, encompassing all uses of plants by any people, from New York City to New Caledonia. For exam-

Shaman and healer Javier Zavala prepares the "rosa-risa" medicinal drink in Tarapoto, Peru. Made from the *Ayahuasca* plant and organic tobacco juice, the mixture is a hallucinogen that also serves to purge the stomach.

ple, the journal *Economic Botany* routinely contains research articles ranging from the use of fungi for medicinal purposes by Amazonian indigenous peoples to the chemical composition of palm seed oils with respect to potential industrial application. In this article, *economic botany* is considered to be synonymous with ethnobotany, and the latter term will be used hereafter.

Changing Approaches

The term "ethnobotany" was first used in a lecture by University of Pennsylvania botanist John W. Harshberger in 1895, but scholarly interest in the utility of plants goes back to the beginnings of botany, and practical interest goes back to the beginnings of civilization itself. Initially to survive, and then for civilization to develop, people needed to learn what plants were useful for foods, fuels, medicines, and fibers and how such plant resources could be mined or managed for human benefit. Harshberger's 1896 publication, *The Purposes of Ethnobotany*, marks the beginning of this academic discipline. Practitioners before and since have approached the subject from widely varying perspectives, resulting in a fluid and rapidly evolving discipline, but one with theoretical underpinnings that are still in their infancy.

Early in the twentieth century, two principal approaches to the study of plants and people developed, and it is not an oversimplification to state that one approach emphasized the "ethno" while the other focused on the "botany." Ethnobotanical studies conducted by botanists tended to be lists of plants arranged by scientific and common names with short commentary on the purpose for which the plants were used, but often with little or no information on how plant resources were managed or fit into people's lives. Anthropologists, on the other hand, were much more concerned with the cultural role of plants in people's lives, but generally only scant attention was paid to the botanical documentation of plant species being studied. One deficiency of some early ethnobotanical studies that did not cross-reference the name of a plant reported with a **specimen** deposited in an herbarium was that such studies were not reliable, as there was no way for subsequent researchers to confirm the identification or name of a plant cited. Not surprisingly, it was only when scientists of different disciplines began to col-

specimen object or organism under consideration

laborate with each other on ethnobotanical studies that more compete pictures began to emerge on the relationships between plants and people. In the twenty-first century, ethnobotany is characterized by being an interdisciplinary, dynamic endeavor, one that combines great intellectual challenge with tremendous practical urgency in terms of the conservation of biological and cultural diversity.

Aside from the great intellectual components to ethnobotany, the discipline is of more than academic interest. The contribution of plants to human welfare is beyond calculation. Suffice it to say, without plants there would be no people. It is impossible to overstate the importance of the contributions that ethnobotanists have made in collecting information about plants and fungi from indigenous peoples around the world. Dozens of modern medicines, such as pilocarpine, which is used for treating glaucoma, have active ingredients that came to light through ethnobotanical investigations. Hundreds of foods, fuels, fibers, and fragrances have been discovered by ethnobotanists through their investigations into the relationship between plants and people. It makes sense that indigenous people, who have experimented with using organisms in their natural environment for centuries, or even millennia, would never have survived to the present day if they had not figured out what components of the biosphere were useful, or, conversely, harmful. Ethnobotanists are basically studying the success stories in people's use and attempts to sustain nature, a topic of great and timely importance.

Great efforts are now being put into the prospecting for new commercial products from nature, and this activity, variously termed **biodiversity** prospecting or chemical prospecting, is now a major activity, supported by governments and industry. The activity is usually associated with the search for new patent medicines, but it applies equally to the search for new, naturally derived products of any sort; for example, a perfume company might undertake a program of searching for new fragrances from the rain forest, using indigenous people's knowledge of floral aromas as a starting point.

biodiversity degree of variety of life

Of equal importance are the activities of ethnobotanists that relate to understanding how local people manage their biotic resources; this research has great applicability to land use managers, conservation policymakers, and, of course, to local peoples themselves, as often the very act of documentation of resource use by scientists gives legitimacy to local people's tried-and-true management methods. This approach, when the conservation of biodiversity is factored into the equation, has been termed the "New Environmentalism" by renowned Harvard University biologist Professor Edward O. Wilson: "The race is on to develop methods, to draw more income from the wildlands without killing them, and so to give the invisible hand of free-market economics a green thumb." Ethnobotanists have a major role in developing the New Environmentalism as a strategy for managing biodiversity and maximizing its conservation, with efforts to make such efforts truly sustainable being the most elusive component.

Methods of Ethnobotany

Until the 1990s, there existed no widely available references on how ethnobotanical studies are conducted; students largely had to work under the supervision of an established researcher and/or figure out methodology through trial and error. This situation has now greatly improved, and aspiring ethnobotanists can consult Miguel N. Alexiades's *Selected Guidelines* *for Ethnobotanical Research: A Field Manual* (1996) and Gary J. Martin's *Ethnobotany: A Methods Manual* (1995). Central to the conduct of ethnobotanical studies is the researcher's understanding of the professional ethics of the situation, and this involves openness and honesty in dealing with the people whose use of plants is being studied, collaborating scientists, government officials, project funding agencies, and all other stakeholders in the dynamic field research process. Ethnobotanists occupy a special position in the middle, serving as brokers of a sort, dealing on one hand with other scientists, policymakers, and funders, and on the other hand with people who may be among the least powerful in society, and for whom the ethnobotanist has a special responsibility in terms of respecting their confidentiality and trust.

Ethnobotanists tend to have their intellectual roots in one or more traditional academic discipline, such as botany or anthropology. Formal training equivalent to a double major in college is a good preparation. A graduate degree is practically required to secure employment as an ethnobotanist. As ethnobotany has become more interdisciplinary, the most interesting and vital studies are increasingly being done by researchers who have training in, for example, medicine and botany, or anthropology, economics, and botany, or informatics, botany, and geography. Obviously, no one individual can possibly encompass the range of disciplines represented in ethnobotany, but students should at least strive to be as broadly trained as possible, at least in the understanding of and appreciation for diverse approaches.

There are a number of practical considerations that an ethnobotanist should keep in mind in anticipation of conducting field research. It certainly helps to be in good physical condition, as fieldwork is often conducted in physically challenging locales and with local people who are fully adapted to those difficult conditions. Assuming the ethnobotanist can keep up with the people he or she wants to interview and learn from, the next consideration is linguistics. Ideally, the ethnobotanist will learn to speak as much of the relevant local language as possible. A less desirable but workable situation is to arrange for interpreters to assist with interviews, keeping in mind that the saying "things can get lost in the translation" has a basis in reality. Aside from the general trait of having a curious, analytic mind, which would describe most successful scientists, additional essential qualities that are required of ethnobotanists are those of patience, as information is usually gathered in a slow, methodical manner, and flexibility, as things rarely work out as planned. Ethnobotany has a large role in elucidating the information about the plant and fungal kingdoms that is needed by science and society. It is a dynamic, intellectually stimulating and rapidly evolving discipline, and one that holds much promise for shedding light on solutions to the crisis in biological diversity. SEE ALSO AGRICULTURE, HISTORY OF; MEDICINAL PLANTS; NATIVE FOOD CROPS; PLANT PROSPECTING; PSYCHOACTIVE PLANTS.

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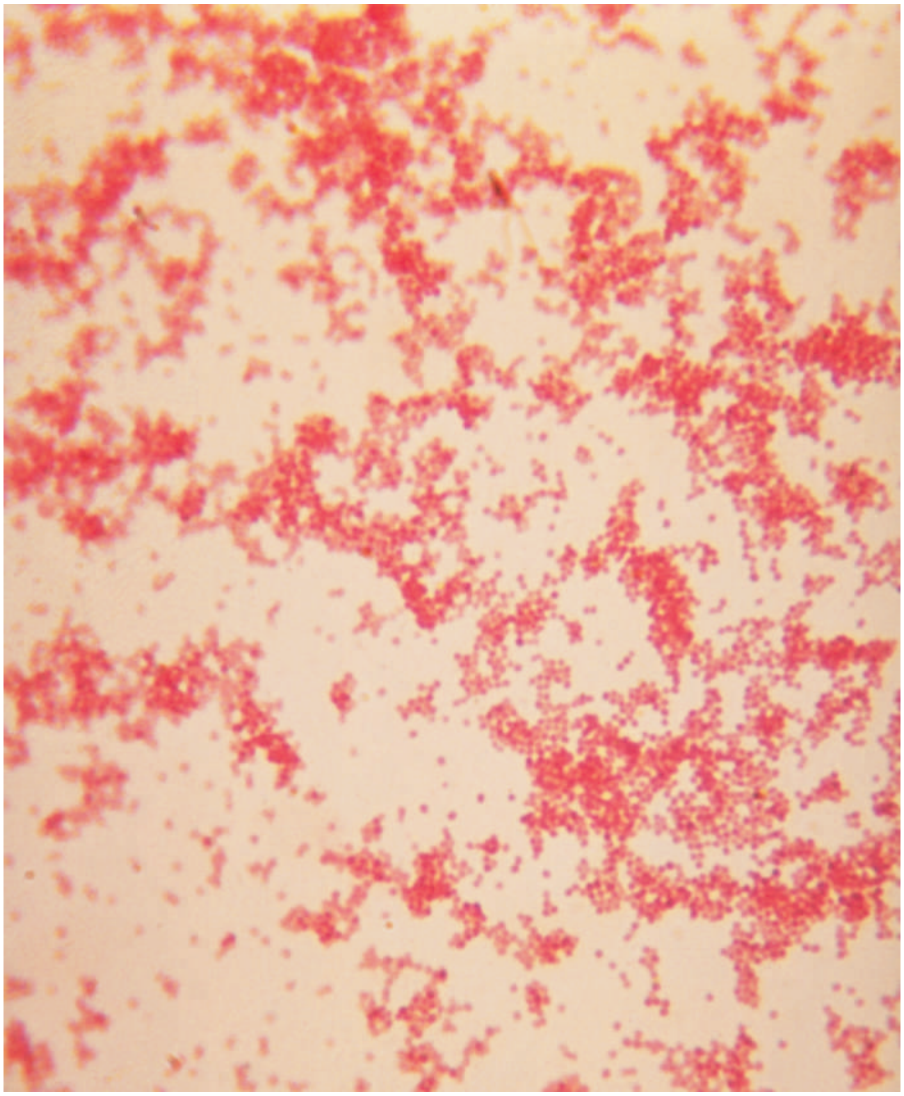
Ethylene *See Hormones.*

Eubacteria

Eubacteria (more commonly known as bacteria) are **prokaryotic** microorganisms that can be found almost everywhere on Earth. They are usually single cells but can also be found in chains, **filaments**, or multicellular clusters. Most are about 1 micron (1 μm), or one millionth of a meter in length, although some of the largest can be up to half a millimeter (500 μm). They come in a variety of shapes such as rods, filaments, spirals, vibrio (comma-shaped), and cocci (ball-shaped). Some have stalks that can be used for attachment. Many of them can move by gliding or by rotating small, pro-

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

filament a threadlike extension



Cocci-shaped eubacteria.

jecting filaments called **flagella**. They lack the complex intracellular motility and **mitosis** found in **eukaryotic** cells.

flagella threadlike extension of the cell membrane, used for movement

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

protist usually a single-celled organism with a cell nucleus, of the kingdom Protista

organelle a membrane-bound structure within a cell

chloroplast the photosynthetic organelle of plants and algae

Cellular Structure

Bacterial cells are fairly simple in structure when compared to the eukaryotic cells of fungi, **protists**, plants, and animals. As seen with an electron microscope, the majority of bacterial cell volume is filled with ribosomes, the sites of protein synthesis. Some bacteria, such as those that are photosynthetic, contain many internal membranes where metabolic processes take place. They contain no internal **organelles**, such as mitochondria and **chloroplasts**. Like archaea, bacteria have a prokaryotic cell organization: their deoxyribonucleic acid (DNA) is loosely gathered into a nucleoid and is not surrounded by a nuclear membrane, like that found in Eukaryotes. The DNA usually occurs as a single long circular strand, but some bacteria have linear chromosomes or divide their genetic material into several DNA molecules. Although they are different from the chromosomes of Eukaryotes, the large circular or linear prokaryotic DNA molecules are often termed chromosomes as well. Bacteria can also have smaller circles of DNA called plasmids, which usually carry a small number of genes used for specific metabolic functions—for example, to allow bacteria to metabolize certain compounds. Plasmids can easily be passed from cell to cell, allowing bacteria to rapidly pick up new metabolic functions, and are the basis for many advances in genetic engineering.

covalent held together by electron-sharing bonds

Like all living cells, bacteria are surrounded by lipid membranes. Most bacteria also have cell walls made up of a peptidoglycan called murein. The peptidoglycan layer is made up of a single kind of molecule from **covalently** linked sugar derivatives and amino acids. This molecule surrounds the bacterial cell like chain mail armor. Together with the osmotic pressure, the wall gives cells rigidity and shape. The cell wall structure and the presence or absence of a second lipid membrane surrounding the murein layer determine how bacteria react in a procedure called the Gram stain. Gram-positive organisms, which take up Gram stain, have a single membrane and a very thick outer peptidoglycan layer. Gram-negative organisms do not take up the stain and have two membranes in between which is a thin layer of peptidoglycan.

Distribution and Ecological Roles

Although bacteria may appear simple, they excel in the diversity and complexity of their metabolic capabilities and they are able to survive in many places. Bacteria are found everywhere on Earth where life is able to exist. They are plentiful in soils, bodies of water, on ice and snow, and are even found deep within Earth's crust. They often take advantage of living in and on other organisms in symbiotic relationships and can be found inhabiting the intestinal tracts and surfaces of animals, including humans. For the most part, the bacteria in and around us bring us more benefit than harm. Sometimes however, bacteria can be pathogenic, or disease causing. This can happen for a number of reasons, such as when the host has a compromised immune system or when a bacterium acquires genes that make it grow more aggressively or secrete **toxins** into its host environment.

toxin a poisonous substance

Oxygen-producing photosynthesis, which is so familiar in plants, is actually a bacterial invention. Many bacteria are photosynthetic and use light energy to turn CO_2 from the atmosphere into cell material. Among these only the **cyanobacteria** produce oxygen during photosynthesis. Plastids, the photosynthetic organelles found in plants and algae, evolved from cyanobacteria through a process called endosymbiosis, in which cyanobacteria lived inside the cells of other organisms that were the ancestors of green algae. Mitochondria, found in most eukaryotic cells, also evolved from nonphotosynthetic respiring bacteria in this way.

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

Bacteria are crucial for the cycling of elements necessary for all life. Through various processes, which we generally call decomposition, bacteria break down the cell materials of dead organisms into simpler carbon-, phosphorus-, sulfur-, and nitrogen-containing nutrients that can be used again by other organisms for growth. Without bacteria to recycle these essential nutrients, they would remain within the dead organisms or sediments and would thus be unavailable for use by other organisms. SEE ALSO ARCHAEA; BIOGEOCHEMICAL CYCLES; CYANOBACTERIA; DECOMPOSERS; ENDOSYMBIOSIS; EVOLUTION OF PLANTS; NITROGEN FIXATION.

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Evolution of Plants

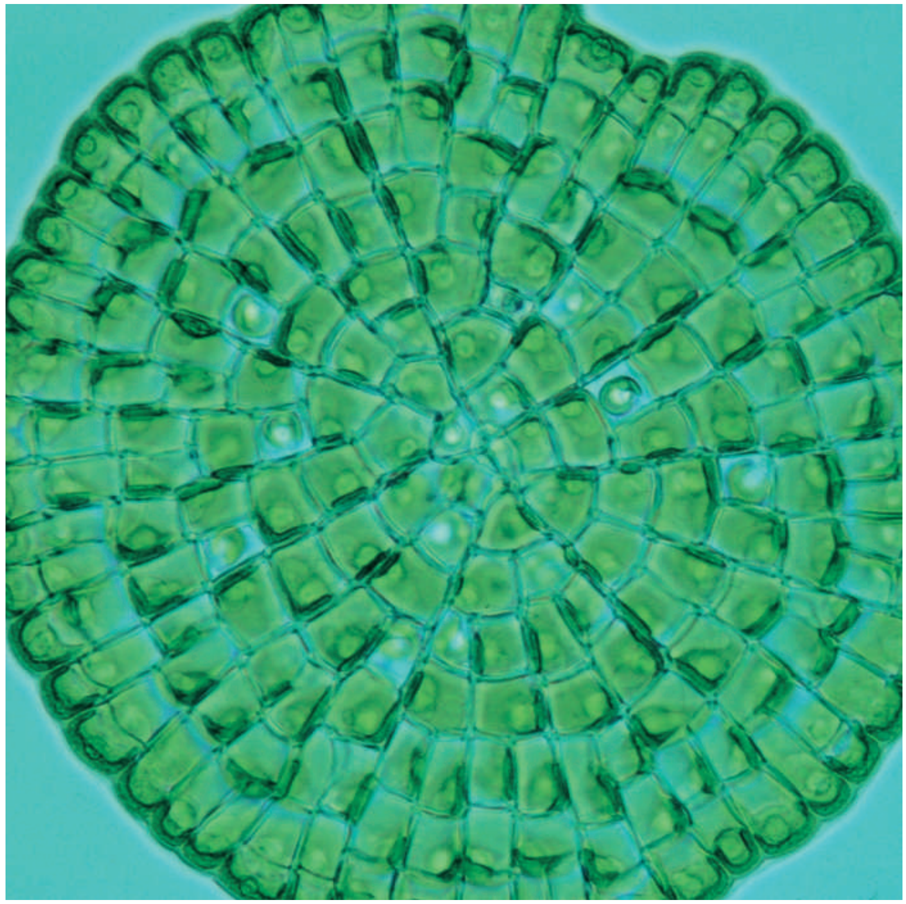
Plants, descended from aquatic green algal ancestors, first appeared on land more than 450 million years ago during or prior to the Ordovician period. This event preceded the colonization of land by four-footed animals (tetrapods), which occurred considerably later in the Devonian period (408 to 360 million years ago). Understanding the origin of plants is important because early plants were essential to the development of favorable terrestrial environments and provided a source of food for animals. In addition, the earliest plants were ancestral to all of the food, fiber, and medicinal plants upon which modern humans depend. The hominid **lineage**, leading to modern humans, is only about 4 million years old; most modern plant community types are considerably older.

lineage ancestry; the line of evolutionary descent of an organism

Ancient, microscopic fossils and deoxyribonucleic acid (DNA) evidence indicate that the earliest land plants resembled modern bryophytes, the liverworts, hornworts, and mosses. Bryophytes are smaller and simpler than other plants. Other larger and more complete fossils reveal that plants became increased in size, and their structure and reproduction became much more complex during the Silurian and Devonian periods (438 to 360 million years ago). The ancestors of today's **vascular** and seed plants appeared during this time. During the Carboniferous period (360 to 286 million years ago) the warm, moist climate favored the growth of extensive, lush forests of ferns and other tree-sized vascular plants. These forests had a dramatic effect on Earth's atmospheric chemistry, resulting in a large increase in oxygen and a drastic reduction in carbon dioxide. The consequent reduction in greenhouse warming caused the climate to change to cooler, drier conditions in the Permian (286 to 248 million years ago), and fostered the rise of the seed plants known as **gymnosperms**. The gymnosperms continued to dominate through the Mesozoic era (248 to 65 million years ago), provid-

vascular related to transport of nutrients

gymnosperm a major group of plants that includes the conifers



An example of a more complex charophycean green alga, *Coleochaete.* This alga is about the size of a pencil point and grows in shallow lakes and ponds, attached to rocks or higher plant stems and leaves. It has many plant-like features.

ing sustenance for giant, herbivorous dinosaurs. Although flowering plants, known as angiosperms, were present by the Cretaceous period (144 to 65 million years ago) and were quite diverse late in this time frame, they shared dominance with gymnosperms until the famously destructive Cretaceous/Tertiary comet or asteroid impact about 65 million years ago. As a result of this event, many previously successful plant groups (as well as dinosaurs and other animals) became extinct. This created new opportunities for flowering plants, mammals, and birds, which consequently became very diverse.

molecular systematics the analysis of DNA and other molecules to determine evolutionary relationships

phylogenetic related to phylogeny, the evolutionary development of a species

Much of what we know about the origin and evolutionary diversification of plants comes from **molecular systematics**, the comparative study of DNA extracted from modern plants. This information allows botanists to construct phylogenetic trees, which are branched diagrams from which evolutionary events can be inferred. **Phylogenetic** trees can also be constructed from structural data, including information from fossils, in order to understand plant evolution. The study of fossils is important because many groups of extinct plants have left few or no close modern relatives from which DNA can be obtained.

The Origin of Land Plants

DNA, structural, and biochemical evidence has conclusively pinpointed a particular group of freshwater green algae known as the charophyceans as the modern organisms that are most closely related to the earliest plants, and have also revealed important steps in plant evolution. Bodies of the most basic charophyceans are either single-celled or form simple groups of cells. Other charophyceans more closely related to plants, according to DNA data, are more complex in their structure and reproduction. These include *Coleochaete* and Charales, a group that is commonly known as stoneworts. The comparison of simple to more complex charophyceans has revealed the origin of several important plant attributes, including: cellulose cell walls; intercellular connections known as **plasmodesmata**; and the **phragmoplast**, a specialized system of components necessary for plant cell division.

plasmodesmata intercellular connections that allow passage of small molecules between cells

phragmoplast the structure from which the cell plate forms during cell division in plants

DNA evidence also marks liverworts as the modern land plants that appeared earliest; liverworts have the simplest plant bodies and reproduction of all plant groups. The ancient microfossils thought to represent the remains of the earliest plants are very similar to the components of modern liverworts. However, the order in which various bryophyte groups appeared is somewhat controversial; some experts argue that hornworts may have come first. Nonetheless, most experts are agreed that mosses are the latest-appearing group of bryophytes and that they are most closely related to vascular plants.

The balance of evidence strongly indicates that all of the modern land plants are derived from a single common ancestor (i.e., they are **monophyletic**), and that this ancestor resembled modern *Coleochaete* and Charales. DNA and other evidence do not support earlier ideas that various modern plant groups evolved independently from different charophycean ancestors. Because modern-day charophycean algae occupy primarily fresh waters, the direct ancestors of land plants are thought to have also been fresh water algae; plants did not arise from ocean seaweeds, as was once thought.

monophyletic a group that includes an ancestral species and all its descendants

The comparison of *Coleochaete* and Charales to bryophytes, particularly liverworts, has revealed much about the evolutionary origin of plant features that contributed to the ability of the first plants to survive on land. These include reproductive spores that are covered with a resistant material known as sporopollenin, which allows them to be dispersed in the air without dying. An apical (top) region of young, dividing cells (**meristem**) that produces a body composed primarily of tissues, reduces the amount of plant surface area exposed to drying. A multicellular **sporophyte** (spore-producing) body enables plants to reproduce efficiently on land. In plants, sporophytes are always associated with parental gametophytes (the gamete-producing bodies) for at least some time in their early development, which is known as the embryonic stage. This combination of sporophyte and **gametophyte** in the life cycle is known as *alternation of generations.* Plant embryos are able to obtain food from the body of their female gametophytes via tissue known as placenta. A placenta is found at the junction of the embryonic sporophyte and gametophyte bodies in all plant groups. The plant placenta is analogous in location, structure, and function to the placenta of mammals. In both mammals and plants, the placenta increases the ability of the parent to produce more young.

meristem the growing tip of a plant

sporophyte the diploid, spore-producing individual in the plant life cycle

gametophyte the haploid organism in the life cycle

Charophycean algae lack sporophytes, tissue-producing meristems, and walled spores. However, they do have precursor features: sporopollenin (though not produced around spores), regions formed of tissues (though these are not extensive and are not produced by an apical meristem), and a placenta (though this supports development of a unicellular **zygote** rather than a sporophyte). The plant sporophyte body is thought to have origi-

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

nated from the charophycean zygote. Comparison of charophyceans with bryophytes illustrates the evolutionary concept of *descent with modification;* features inherited by the first land plants from ancestral charophyceans became modified under the influence of terrestrial environments. Comparative studies of modern charophyceans and bryophytes are needed because no fossils are known that illuminate the algae-to-plant transition, which likely occurred in the early Ordovician or the Cambrian (590 to 505 million years ago) periods.

Plants, including bryophytes and vascular plants, are widely known by the term *embryophytes* because they all have a multicellular, nutritionally dependent embryo (young sporophyte). Synonyms for embryophytes include the term *metaphyta*, which corresponds to the term *metazoa* for members of the animal kingdom. The term *plant kingdom* has been used in a variety of ways by different experts; some restrict this term to embryophytes, some include green algae, and others include brown and red algae as well.

Diversification of Plants

Sometime after the origin of the first plants, bryophytes diversified into the three main modern lineages (liverworts, hornworts, and mosses) and possibly other groups that have since become extinct. Some experts think that bryophytes diversified during the Ordovician period (505 to 438 million years ago). Others are skeptical, because fossils of bryophytes that are sufficiently intact to be sure of their identity are much younger, occurring after the earliest fossils of vascular plants. This is usually explained as the result of the reduced ability of delicate bryophyte bodies to survive damage and decay after death, and the fact that Ordovician deposits are not as well studied as those of later periods. The DNA evidence that bryophytes appeared before vascular plants is very strong. It discounts earlier beliefs, based on the sparse early fossil record, that bryophytes might be descended from vascular plants.

Origin of vascular plants required three important evolutionary advances: (1) sporophytes became able to grow independently of their parents after the embryonic stage; (2) sporophytes were able to branch; and (3) sporophytes acquired lignin-walled vascular tissues. Lignin is a tough, plastic-like material that is deposited in the walls of vascular plant conducting cells, making them stronger and less likely to collapse.

In contrast to vascular plants, bryophyte sporophytes remain dependent on parental gametophytes throughout their lives. Bryophyte sporophytes are unable to branch, so they can produce only one organ that generates spores, the sporangium. Although many bryophytes possess conducting tissues, these lack lignin in their walls. Modern (and fossil) vascular plants, also known as tracheophytes, have branched sporophytes that at maturity are (were) able to grow independently of gametophytes. Independent growth allows tracheophyte sporophytes to live longer than those of bryophytes. Branching vastly increases reproductive potential because many more sporangia and spores can be produced. **Lignified** vascular tissues provide a more efficient water supply and greater mechanical strength, giving vascular plants the potential to grow much larger than bryophytes. Woody plants contain large amounts of lignified conducting tissues—the strength and durability of wood derives largely from its lignin content.

lignified composed of lignin, a tough and resistant plant compound

The hornwort *Anthoceros* has a very simple, flat inconspicuous gametophyte body, with more obvious elongate sporophytes growing from it. This plant commonly occurs in muddy places, but the sporophytes, which resemble clumps of small grass blades, are only visible in early spring.

The fossil record reveals that there were ancient plants that had many of the features of bryophytes, including absence of vascular tissues, but whose sporophytes were branched and capable of living independently at maturity like those of vascular plants. These plants lived in the late Silurian (about 420 million years ago) and into the Devonian period, then became extinct. Known only as fossils, these plants are described as *pretracheophyte* (meaning "before vascular plants") *polysporangiates* (meaning "producing many sporangia"). They are represented by fossils such as *Horneophyton* and are viewed as possible intermediates between bryophytes and vascular plants. They are also interesting because their sporophyte and gametophyte bodies were of similar size and complexity, in contrast to bryophytes (in which gametophytes are usually larger than sporophytes) and vascular plants (whose sporophytes are larger and more complex than gametophytes).

Fossils show that there were early vascular plants that had primitive lignified conducting cells. Later-appearing fossils and modern vascular plants are known as *eutracheophytes* because they have more complex conducting cells. Modern vascular plants are thought to be derived from a single common ancestor. The comparative study of fossil and modern vascular plants has been valuable in understanding the evolutionary origin of vascular tissues, leaves, and seeds.

Lycophytes. Fossil and DNA evidence indicates that the lycopsids were an early group of eutracheophytes; these include modern nonwoody (herbaceous) plants known as lycophytes (*Lycopodium*, *Selaginella*, and *Isoetes*) and extinct trees that dominated the coal swamps of the Carboniferous period (360 to 286 million years ago), producing extensive coal deposits. Modern and fossil lycopsids have (had) small leaves with just a single, unbranched vein, which are known as **microphylls**. It is amazing that the Carboniferous lycopsids were able to grow to such prodigious sizes and numbers since they only had tiny leaves with which to harvest sunlight energy. They did not produce seeds.

microphylls small leaves having a single, unbranched vein

Ferns and Horsetails. Later-appearing plants include ferns, the horsetail *Equisetum*, and seed plants; these plants have leaves with branched veins.

megaphylls large leaves having many veins or highly branched vein system

Leaves that have veins that branch, and thus are capable of supplying a larger area of photosynthetic cells, can become quite large and are consequently known as megaphylls. **Megaphylls** are an important adaptation that allow plants to harvest greater amounts of sunlight energy. Ferns, horsetails, and seed plants, as well as some extinct plants known only as fossils, are grouped together to form the *euphyllophytes* (meaning *plants with true or good leaves*). It is thought that megaphylls might have evolved separately in seed plants and ferns from separate ancestors that both had systems of branches called *megaphyll precursors*. The processes of planation (the compression of a branch system into a single plane) and webbing (the development of green, photosynthetic leaf tissue around such a branch system) are evolutionary stages in the origin of leaves that may have occurred independently in ferns and seed plants. This is another good example of *descent with modification*, and it illustrates the fact that similar changes often occur independently in different plant groups because they confer useful properties (convergent evolution). Leaves of one kind or another are thought to have evolved at least six times, in different plant groups.

Gymnosperms. Gymnosperms arose from a now-extinct group called the progymnosperms. Progymnosperms are represented by fossils such as *Archeopteris*, a large forest-forming tree that lived from about 370 to 340 million years ago and had megaphylls. Gymnosperms were dominant during the Permian period (286 to 248 million years ago), a time of cool, dry conditions for which gymnosperms were generally better adapted than many ferns and lycophytes. Adaptations that facilitate survival in cool, dry conditions include leaves that have reduced surface area (i.e., are needle or scale-shaped) and seeds. Reduced leaf surface area helps reduce the loss of water by evaporation. Having seeds reduces a plant's dependence on liquid water to accomplish fertilization during sexual reproduction and allows seed dormancy, the ability of the protected embryo to persist until conditions are favorable for germination. Today, gymnosperms are still quite successful in cool and dry environments, such as forests of high latitudes (taiga) and mountains. There were some ancient seed-producing ferns that do not seem to be related to any modern group. These ferns illustrate independent origin of seeds and the value of seeds as an adaptation.

The origin of modern seed plants was accompanied by the first appearance of embryonic roots (radicles). In contrast, nonseed plants lack an embryonic root, rather, roots arise from the adult stem, often from a kind of horizontal stem known as a rhizome.

Angiosperms. The origin of the first flowering plants is not well understood, and it is a topic of great interest to botanists. Progymnosperms and the Gnetales, an unusual group of modern gymnosperms, are thought by some experts to be closely related to angiosperms. However, DNA evidence has cast doubt on the connection to Gnetales. DNA evidence also indicates that the most primitive modern flowering plant is *Amborella*, a native of the Pacific island New Caledonia. Researchers are working to understand the origin of the unique and defining features of flowering plants, including flowers, fruits, and seeds with **endosperm**. The evolutionary radiation of flowering plants is associated with coevolution—the coordinated evolutionary divergence of many animal groups, including insects, bats, birds, and mammals. Animals depend on these plants as a source of food and play im-

endosperm the nutritive triploid tissue formed in angiosperm speeds during double fertilization portant roles in carrying spores (pollen) between plants and transporting fruits and seeds to new locations. The extinction of any modern flowering plant could thus potentially cause animal extinctions, and vice versa.

There are at least 3,000 living species of charophyceans, primarily desmids living in peat bogs dominated by the moss *Sphagnum.* Species of living plants are estimated to include 6,000 liverworts, 100 hornworts, 9,500 mosses, 1,000 lycophytes, 11,000 ferns, 760 gymnosperms, and 230,000 angiosperms. New species are continuously being discovered. SEE ALSO Algae; Angiosperms; Bryophytes; Evolution of Plants, History of; Gymnosperms; Phylogeny; Seedless Vascular Plants; Systematics, Molecular; Systematics, Plant.

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Evolution of Plants, History of

The conception that living organisms are changing or mutable originated in the thoughts of Empedocles, an ancient Greek philosopher (c. 490–430 B.C.E.). He drew on the theories of Greek philosophers preceding him to suggest a unitary view of the world consisting of the four elements of earth, air, fire, and water, which interacted with each other according to the principles of love (attraction) and strife (repulsion). Organisms arose from varying combinations of the elements under the action of either love or strife. Thus organic (living) entities were thought to arise from inorganic (nonliving) materials, which then became adapted through a process of selection to their environment. Empedocles not only applied this theory to the origin of plants, but stated that they were the first living organisms.

From Aristotle to Lamarck

This evolutionary worldview was put on hold by the theories of the great Greek philosopher Aristotle (384–322 B.C.E.) and by his famous student Theophrastus (c. 372–287 B.C.E.), who is regarded as the father of scientific botany. They believed in a fixed or static universe, which saw all plants and animals as falling into discrete types or kinds organized in a well-defined, hierarchical scheme from lower to higher organisms. Aristotle called this organization of life, the *scala naturae*, or the ladder of creation. This view dominated natural philosophy and reached its fullest expression with the work of the great Swedish taxonomist, Carolus Linnaeus (1707–1778). His reform of the taxonomic system was built on the idea that organisms such as plants fall into well-defined types. The Linnaean system follows this typological or essentialistic approach to the natural world by adhering to the notion of the ideal type. This is seen in the pivotal taxonomic use of the type **specimen**, the technical taxonomic term for the first species of a new group described.

specimen object or organism under consideration

The return to a changing vision of life accompanied the new geological theories of the eighteenth century. These new theories were fueled by new fossil discoveries and the establishment of the view that fossils are organic in nature; that is, that they were remnants of once-living organisms. Plant fossils figured prominently in this. Geological theories were also informed by the revolutionary beliefs associated with the **Enlightenment,** especially the idea of progress. This idea implied a directionality to history and suggested that progress was in the natural order of things. It also suggested that the world, and Earth, were much older than previously thought, especially as revealed by Biblical scripture. Combined with developments in the comparatively new **morphology** of both plants and animals and the staggering diversity of new specimens of plants and animals flooding Europe from the voyages of discovery, the new geological theories began to uphold the view that Earth changed in a slow, gradual manner. Instead of accepting the view of unique, one-time, or catastrophic events—such as the flood of Noah—the view that uniform geological processes were responsible for creating Earth, or uniformitarianism, began to dominate geology. Soon, naturalists began to challenge the notion of the fixity of species as they realized that Earth itself was undergoing constant but uniform change.

Enlightenment Eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

morphology shape and form

The French naturalist Comte Georges-Louis Leclerc de Buffon (1707–1788), a contemporary of Linnaeus, was one of the first to suggest a **transmutationist** theory for living organisms. He made a famous speculative statement applying his belief in a constantly changing Earth to living organisms in volume three of his great compendium of the natural history of Earth, *Histoire naturelle* (1749–67). This statement paved the way for the first coherent transmutationist theory formulated by Jean Baptiste Lamarck (1744–1829), a botanist of some repute, and the first person to use the word "biology." This theory was clearly formulated in his *Philosophie zoologique* (1809). Despite its zoological title, the book drew on insights Lamarck had gleaned from his botanical background to explain the phenomenon of adaptation in all living organisms. According to Lamarck, favorable adaptations were originated by the effect of the environment acting directly on the organism. Lamarck therefore mistakenly thought that the environment directly induces permanent change in the genetic composition of organisms. This was what he meant by the "inheritance of acquired characters." The phenomenon of use and disuse, also associated with Lamarck, stated that prolonged use of an organ led to its modification, and disuse led to its elimination. Although Lamarck's theory was widely discussed and became especially popular in his native France, it did not provide a mechanism for how the environment induced such permanent modification, nor did it provide good scientific evidence.

transmutation change from one form to another

Darwin, Mendel, and the Evolutionary Synthesis

These inadequacies were addressed by the individual who is most closely associated with the theory of organic evolution, Charles Darwin (1809–1882). Darwin did not explicitly reject Lamarck's explanation for adaptation, but instead suggested another mechanism he called natural selection. This was the process by which organisms with favorable variations survived to reproduce those favorable variations. Given enough time, he argued, subsequent generations would depart from the parental type under the action of selection until they formed a new species. This principle of divergence supported and strengthened what Darwin formally called his "theory of descent with modification." This theory was set forth in *On the Origin of Species* (1859). Darwin drew heavily on examples from the distribution of plants and on knowledge of plant breeding to formulate his theory. In the last twenty years of his life, he studied the phenomenon of adaptation in plants such as orchids, which had evolved spectacular contrivances by which to attract pollinators such as bees. Plants were in fact to provide Darwin with some of the best evidence in support of his theory.

Darwin's theory of evolution transformed understanding of the origins of all life on planet Earth. Botanists such as Joseph Dalton Hooker (1817–1911) in England and Asa Gray (1810–1888) in the United States grew to accept and apply Darwinian evolution to the plant kingdom and to promote the theory further. Despite its success, a considerable number of botanists continued to uphold Lamarckian notions well into the twentieth century. One reason for this is that it is especially hard to distinguish between genotypical variation (variation due to genetics), and phenotypical variation (variation as the result of a direct response to the environment). Unlike animals, which have closed developmental systems, plants have open or indeterminate developmental systems that permit them to continue to "grow" and generate new tissue in regions such as the shoot and root. Plants are thus able to demonstrate the phenomenon of phenotypic plasticity, the ability to adapt readily to new environments and to generate especially complex variation patterns that appear to support Lamarckian inheritance.

It took the work of the geneticists such as Gregor Mendel (1822–1884), who formulated the modern theory of heredity, and Wilhelm Johansen (1857–1927), who first drew the distinction between phenotype and genotype, to begin to understand more complex aspects of plant evolution, such as plant **speciation**. It was not until 1950, however, that botanists were able to finally integrate Darwinian natural selection theory with Mendelian genetics, and finally dispelled notions of Lamarckian inheritance. Modern ideas of plant evolution and the science that is framed by the subject, plant evolutionary biology, appeared with the publication of *Variation and Evolution in Plants* (1950), by the American botanist George Ledyard Stebbins Jr. (1906–2000). With its appearance, botany and plant evolution are generally thought to have become part of the historical event termed "the evolutionary synthesis." This event finally saw the establishment of Darwinian evolution by means of natural selection synthesized with Mendelian genetics. It remains the overarching theoretical framework for explaining the evolution of plants. SEE ALSO DARWIN, CHARLES; EVOLUTION OF PLANTS; HOOKER, JOSEPH DALTON; MENDEL, GREGOR.

speciation creation of new species

Vassiliki Betty Smocovitis

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Fabaceae

The Fabaceae family, known as legumes, are one of the most important plant families in both ecological and economic terms. Legumes help increase soil nitrogen and provide rich sources of vegetable protein for humans, livestock, and wild animals.

Structure

The flowers of the legume family are diverse but uniformly bilaterally symmetric. Indeed, fifty-million-year-old fossil legume flowers provide the first instance of bilaterally symmetrical flowers in the fossil record of flowering plants. Most legumes have five petals and five **sepals**, with the sepals commonly fused at least at the base. The five petals commonly occur as one large upper petal, two lower petals that clasp the ovary and stamens, and two **lateral** petals that often act as a platform for a landing bee (or other insect). There are deviations to this pattern, including a common one where petals are all alike and arranged in a radially symmetric fashion even though the ovary or stamens always retain the bilateral symmetry.

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

lateral away from the center

The fruits of the legume family are also varied. Most commonly, one fruit (the pod) is produced per flower. The pod has two valves, each bearing a seed along the upper margin. The two valves together form the single compartment of most pods. When the fruit matures, the two valves often twist apart forcefully, catapulting the enclosed seeds. However, pods of many legume species remain intact and disperse with the mature seed. The seed then germinates from within the fallen pod. The pod may not have a single compartment, but rather can be transversely segmented such that each seed is enclosed in its own compartment. Pods can be small and contain one seed or linear to circular and contain dozens of seeds.

The distinctive aspect to the vegetative **morphology** of legumes is the compound leaf, mostly pinnately compound, but also palmately compound. Less common are simple legume leaves. Legume leaves are deciduous during the dry season in the tropics or during the winter in temperate regions. Deciduous leaves are considered an adaptation to habitats with seasonally varying moisture availability, which is especially the case in many tropical regions.

morphology shape and form

The morphology of the legume fruit is dependent upon how the pod disperses. Water-dispersed fruits have a thick buoyant outer covering that contains many air cells (e.g., *Andira*). Wind-dispersed fruits often bear wings of varying sizes and shapes (e.g., *Dalbergia*). Pods carried away on the fur of passing animals bear different kinds of hairs, ornaments, or glands to make them sticky (*Desmodium*, for example). The structure attaching the seed to the inside of the fruit is sometimes fleshy. This fleshy structure (the aril, as in *Pithecellobium*) is firmly attached to the seed and is often colorful and sweet and serves to disperse the seed (e.g., by birds). Legume seeds are highly variable but always include a preformed embryo with two large cotyledons. The cotyledons are rich in nitrogen compounds (such as alkaloids or nonprotein amino acids), most of which are toxic to animals. Selection during domestication has resulted in the loss of **toxins** while retaining the nitrogen-rich compounds. Legumes cultivated for their edible nitrogen rich seeds (e.g., beans, peas, and lentils) are referred to as pulses. Soybeans form an important part of the diet in Asia and are used as a protein-rich livestock feed in many countries.

toxin a poisonous substance

Distribution, Symbiosis, and Economic Importance

The Fabaceae predominate in most vegetation types of the world. Legume species are most abundant in seasonally dry, tropical forests, but they also abound in high deserts to lowland rain forests. They are notably uncommon in high alpine sites with abundant summer rains and in the southern beech forests of the Southern Hemisphere. Woody legume species are mostly confined to tropical and subtropical habitats, but herbaceous species occur from the tropics to cold temperate regions. Thus, many legume species are available for use in reforestation or revegetation projects worldwide. Their efficient ability to acquire nitrogen, phosphorus, and other essential nutrients, whether through nodulation or association with mycorrhizae (symbiotic root fungi), allows them to easily establish on abused lands where soils are eroded, leached, or acidic. Legumes can be found as pioneer species

ECONOMICALLY IMPORTANT LEGUMES

Common Name	Scientific Name	Uses
Edible (human or livestock)		
Alfalfa, lucerne	*Medicago sativa*	Forage, commercial source of chlorophyll
Alsike clover	*Trifolium hybridum*	Forage
Baked, navy, kidney bean	*Phaseolus vulgaris*	Edible seeds
Carob	*Ceratonia siliqua*	Pods with edible pulp, ornamental
Chick pea, garbanzo bean	*Cicer arietinum*	Edible seed
Faba bean	*Vicia faba*	Edible seeds
Fenugreek	*Trigonella foenum-graecum*	Edible and medicinal seeds, dye
Garden pea	*Pisum sativum*	Edible seed
Japanese clover	*Lespedeza stiata*	Forage, revegetation
Lentil	*Lens culinaris*	Edible seed
Licorice root	*Glycyrrhiza glabra*	Rhizomes a source of licorice
Lima bean	*Phaseolus lunatus*	Edible seeds
Mesquite	*Prosopis glandulosa*	Edible pods, forage, fuel
Mung bean	*Vigna radiata*	Edible seeds and pods
Peanut	*Arachis hypogaea*	Edible seeds
Potato bean, groundnut	*Apios tuberosa*	Edible tuber
Soybean	*Glycine max*	Edible seeds for oil and other products
Tamarind, Indian date	*Tamarindus indicus*	Pods with edible pulp
Vetch, tare	*Vicia sativa*	Forage or green manure
White clover	*Trifolium repens*	Forage
Yam bean, jicama	*Pachyrhizus erosus*	Edible tuber
Yellow sweetclover	*Melilotus officinalis*	Forage
Ornamental		
Black locust	*Robinia pseudoacacia*	Ornamental, timber, reforestation
Crown vetch	*Coronilla varia*	Ornamental, revegetation
Honey locust	*Gleditsia triacanthos*	Ornamental
Kentucky coffee tree	*Gymnocladus dioica*	Ornamental
Lupine	*Lupinus albus*	Ornamental, forage, edible seeds
Redbud	*Cercis canadensis*	Ornamental, edible flowers
Scarlet runner bean	*Phaseolus coccineus*	Ornamental, edible fruits and seeds
Sensitive plant	*Mimosa pudica*	Ornamental house plant
Silk tree	*Albizia julibrissin*	Ornamental
Sweet pea	*Lathyrus odoratus*	Ornamental
Other		
Acacia	*Acacia senegal*	Sap a source of gum arabic
African blackwood, Brazilan rosewood	*Dalbergia nigra*	Luxury timber
Cascolote	*Caesalpinia coriaria*	Source of tannins
Indigo	*Indigofera tinctoria*	Dye, forage
Kudzu vine	*Pueraria lobata*	Revegetation, forage
Peachwood, brasiletto	*Haematoxylum brasiletto*	Timber, dye, ornamental

or as major constituents in secondary vegetation. Disturbed lands characterized by high erosion, leaching of nutrients, or accumulation of salts can become readily inhabited by legume species. Notably, an association of mycorrhizae and legumes is just as important in this regard as is the legume-rhizobia association. This is especially true when soils are acidic. The nitrogen-rich metabolism of legumes is a desired property for revegetation because by killing the legume (naturally or intentionally), nitrogen is released for use by non-leguminous associates. Green manuring a worn-out field with clover, for instance, can help restore soil fertility.

A remarkable feature of the Fabaceae is the high nitrogen metabolism that occurs in all members of this family. Legumes are so nitrogen-demanding that they have evolved several mechanisms to efficiently scavenge organic and inorganic nitrogen from the soil. One of these is the formation of root nodules upon infection by rhizobia. Rhizobia is the collective name for bacteria that infect legume roots and fix atmospheric nitrogen, which then becomes available to the legume plant. Many legumes are susceptible to being infected by rhizobia, whereupon the rhizobia are localized by the legume plant in root, rarely stem, nodules.

Legumes and rhizobia have a symbiotic relationship, which benefits the legume but is not necessary for its growth. Legumes appear to acquire nitrogen by other means than nodulation first, and an influx of soil nitrogen, natural or otherwise, can cause a nodulating legume to cease its association with rhizobia.

Few if any other plant families have as many species that are so economically important worldwide as the Fabaceae. This is especially true for both industrial and nonindustrial economic species. Peas, beans, and lentils (the pulses) are probably the most important industrial species, but luxury timbers (e.g., rosewoods) are also important here. The most economically important nonindustrial species include multipurpose tree species, such as *Leucaena leucocaphala* or *Gliricidia sepium*, which are cultivated for shade in crop fields (as in coffee plantations), local timber, livestock forage, and cover for reforestation projects. Hundreds of herbaceous and woody legume species are cultivated regionally or globally as ornamentals, livestock forage, **green manure**, or as sources of gums, medicinal products, or secondary metabolites. SEE ALSO Biogeochemical Cycles; Kudzu; Nitrogen Fixation; Plant Community Processes; Savanna; Soybean; Symbiosis.

Matt Lavin

green manure crop planted to be plowed under, to nourish the soil, especially with nitrogen

Family

Family is the taxonomic rank between order and genus. A number of related genera make up one family. A number of related families are then grouped into an order, a higher rank that therefore represents a larger group of plants. A family may include only one genus and one species or hundreds of genera and several thousand species. A large family may be further organized using the rank of subfamily, with related genera grouped into subfamilies, then subfamilies into families.

In the past, families and subfamilies were just groups of genera that shared some similar features, especially of the flower and fruit. Such groupings often omitted closely related plants that looked different. Beginning in the late twentieth century, botanists have come to think that families should be natural groups. A natural group, which includes all the descendants of some common ancestor, is based on evolutionary relationships, not just similar appearance.

Names of families can be recognized by the ending "-aceae." Each family has a type genus, a representative genus that defines that family, and the family's name is formed by adding -aceae to the name of that genus. For example, *Primulus* (primrose) is the type genus of the family Primulaceae, or primrose family. SEE ALSO Plant Systematics; Taxonomy.

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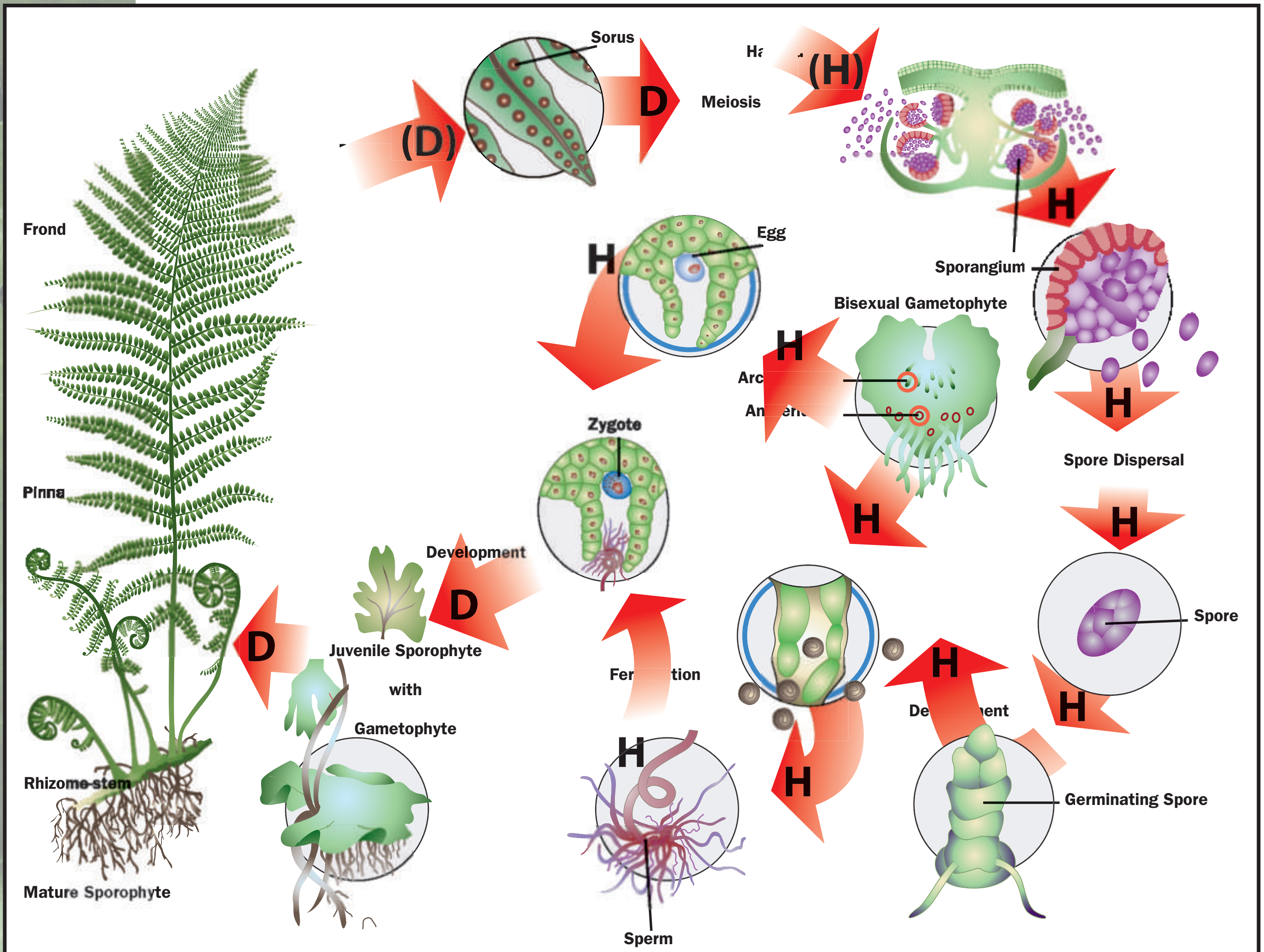
Ferns

Ferns, like the more familiar seed plants, have stems, roots, and large, highly veined leaves. Ferns do not reproduce by seeds, however, and have several other distinctive features. The leaf of a fern is called a frond and, in many species, the green blade is divided into segments called pinnae. The leaves of most ferns have a distinctive juvenile stage called a fiddlehead, where all the segments are curled in a manner resembling the end of a violin's neck. Most ferns have underground stems called rhizomes and the only parts of the fern plant visible above ground are the leaves. Some tropical ferns, called tree ferns, have erect, unbranched stems up to 20 meters tall with all of the fronds arising from the tip. Ferns are perennial plants and some may grow for many years, but, as they lack annual growth rings, their age is not easily determined. However, in 1993, researchers using molecular genetic markers found some individual bracken fern (*Pteridium aquilinum*) plants more than 1 kilometer across. Researchers estimated that these ferns took more than 1,180 years to grow to this size, possibly putting them among the oldest living plants on Earth.

Ferns and seed plants are similar in having two kinds of plants present in their reproductive life cycle, but overall ferns reproduce very differently than seed plants. The familiar fern plant, described in the preceding paragraph, is the **sporophyte** (spore-bearing phase). Fern fronds bear organs known as sporangia. Inside each sporangium certain cells undergo reduction division, or meiosis, which yields haploid spores that have one set of genes for the fern. All of the cells in the sporophyte fern plant itself are diploid, having two sets of genes. The sporangia of most ferns are very small, scalelike, and contain only sixty-four spores, but some ferns have large sporangia containing hundreds of spores. A typical fern sporophyte plant may produce up to one billion spores per year. When the sporangia open, the spores are shed into the air and dispersed. While most fern spores land within one hundred meters of the fern producing them, some may be spread very far. Fern spores have been recovered from the upper atmosphere in samples collected by airplanes and weather balloons.

sporophyte the diploid, spore-producing individual in the plant life cycle



The life cycle of a fern.

substrate the physical structure to which an organism attaches

gametophyte the haploid organism in the life cycle

When the single-celled fern spore lands on a suitable **substrate**, it may undergo mitotic cell division and develop into a very different kind of plant. The plant that grows from a fern spore, called the prothallus, is barely visible to the naked eye. It resembles a tiny, heart-shaped ribbon and lacks any stems, roots, leaves, or internal food- or water-conducting tissues. Reproductively, this small, independent fern plant is critical because it bears the sex organs. Although the basics of sexual reproduction in ferns were discovered in the nineteenth century, many crucial details are still being clarified. A single fern **gametophyte** may produce both sperm-bearing sex organs, called antheridia, and egg-bearing sex organs, known as archegonia, but frequently an individual gametophyte has only one type of sex organ. Fertilization occurs when a sperm swims to unite with an egg to form a diploid zygote, which then develops into the sporophyte.

Whether the individual gametophyte plants in a population are bisexual or unisexual is very important because it is basic to determining the degree of genetic variation possible in the sporophyte generation produced. A single bisexual gametophyte can fertilize its own eggs and produce a new sporophyte plant, but such a sporophyte would be highly inbred because both the sperm and egg producing it would be genetically identical. Most ferns control the sexual expression of the individual plants in a gametophyte population so that each plant is either male or female. Thus, fertilization usually requires two gametophytes that are close enough for sperm to swim in water between them. Receptive archegonia secrete a sperm **attractant** to help the sperm find its way. When genetic material from two different gametophytes is mixed in the zygote, the sporophyte that develops has more genetic variation than one arising from a single gametophyte. If the entire fern sporophyte population is reproduced this way, it may be more likely to survive because some of its members may have inherited the traits needed to endure unforeseen changes in its environment. On the other hand, a distinct survival advantage arises when a single fern spore, dispersed a long distance, can produce a sporophyte from one gametophyte, because this permits rapid colonization of distant, favorable habitats.

attractant something that attracts

Although factors regulating fern spore germination and development are fairly well known from laboratory studies, relatively little is known about how ferns actually reproduce in their environments. Most fern spores germinate readily on moist soil. Germination often requires red light that is absorbed by a pigment in the spore. Calcium ions are important to germination, and red and blue light control the pattern of gametophyte development. Fern spores are known to persist in the soil, forming spore banks. These factors and many more interact in complex ways in the field. Ecologically, most fern species are found in habitats where moisture is readily available, permitting gametophytes to grow and sperm to swim to eggs in water. Those concerned with preserving a rare fern species at a site must understand that if the locality does not provide safe sites for the independent gametophytes, with their distinct ecological requirements, the species cannot reproduce and the sporophytes will eventually die off.

Moist, tropical mountain forest communities contain the largest number of fern species. Of the approximately 12,000 fern species worldwide, about 75 percent are tropical. The flora of North America, north of Mexico, contains about 350 fern species, whereas southern Mexico and Central America have about 900. A few ferns are occasionally eaten. However, some, like bracken fern, contain poisons or carcinogens. Ferns are present in most plant communities but dominant in few. SEE ALSO EPIPHYTES; SEEDLESS VASCULAR PLANTS.

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Fertilizer

Adding nutrients to agricultural systems is essential to enhance crop yield, crop quality, and economic returns. Commercial fertilizers are typically used to supply needed nutrients to crops. Nitrogen (N), phosphorus (P), and

An Amish farmer uses a horse team to spread fertilizer on a field in Lancaster County, Pennsylvania.

potassium (K) fertilizers are used extensively. Other secondary and micronutrient fertilizers are generally required in small quantities to correct plant nutrient deficiencies.

Commercial fertilizers contain a guaranteed quantity of nutrients, expressed as fertilizer grade on a label showing the weight percentage of available N, P_2O_5, and K_2O equivalent (N-P-K) in the fertilizer. Additional nutrients in fertilizer formulations are listed at the end of the fertilizer grade with the nutrient identified. Commonly used commercial fertilizers include ammonium nitrate (fertilizer grade 33-0-0), urea (45-0-0), urea-ammonium nitrate (28-0-0), anhydrous ammonia (82-0-0), diammonium phosphate (18-46-0), monoammonium phosphate (10-52-0), ammonium polyphosphate (10-34-0), ammonium thiosulfate (12-0-0-26S), potassium chloride (0-0-60-45Cl), potassium sulfate (0-0-50-18S), and potassium-magnesium sulfate (0-0-22-22S-11Mg). The secondary plant nutrients sulfur (S) and magnesium (Mg) are often contained in the nitrogen, phosphorus, and potassium fertilizers as shown.

Fertilizers are available in several forms (solids, fluids, and gases), which makes their handling and precise application very compatible with planting and fertilizer application equipment. Fertilizers are applied in several ways; they can be broadcast over the soil surface or in narrow bands on or in the soil, as foliar applications to plants, or through irrigation systems. For more efficient use, fertilizer should normally be applied just prior to the time of greatest plant nutrient uptake. In contrast, organic sources, such as animal manures, need to be applied and incorporated into the soil prior to planting the crop to be most effective.

Management of crop nutrient requirements is easier with commercial fertilizers than with organic fertilizers such as animal manures, bio-solids, byproducts, and other organic waste products. Release of many of the plant nutrients from these sources requires the breakdown of organic material by soil microbes and release of plant nutrients through a process called mineralization. Many of the nutrients from organic sources are not available to plants until this process has occurred. Release of plant nutrients from organic sources may not correspond with the period of greatest crop need.

Organic fertilizers and **legumes** are good sources of nutrients for crop production. Balancing the quantity of nutrient application with organic sources to match crop need is more difficult than with commercial fertilizers. Application of sufficient animal manure to meet crop nitrogen needs will likely result in an overapplication of phosphorus. Conversely, application of sufficient manure to meet the phosphorus needs of crops could result in the under application of nitrogen. Nutrient content of most organic sources is highly variable and needs to be determined before application to soils to avoid overapplication of some nutrients.

legumes beans and other members of the Fabaceae family

Balancing crop nutrient needs using both inorganic commercial fertilizer and organic sources is an excellent way to avoid overapplication of plant nutrients. Soil and/or plant tissue testing should be used to determine crop nutrient needs before applying nutrients from any source. This will ensure efficient use of plant nutrients while maintaining high crop yields, crop quality and profitability, and preserving or enhancing environmental quality. SEE ALSO Agriculture, Modern; Biochemical Cycles; Compost; Nutrients; Organic Agriculture; Soil, Chemistry of; Soil, Physical Characteristics of.

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Fiber and Fiber Products

Fibers are strands of cells that are characterized by an elongate shape and a thickened secondary cell wall composed of cellulose and hemicellulose. Dead at maturity, fiber cells possess tapered, overlapping ends that form long, multicellular fibers. These fibers impart elastic strength to stems, leaves, roots, fruits, and seeds of flowering plants. Most fiber cells arise from vascular tissues and are commonly found in association with phloem tissue, although fibers may also be found in xylem or independent of **vascular** tissue. Fiber cells typically incorporate lignin in their secondary wall, a substance that creates additional stiffness in fiber cells.

vascular related to transport of nutrients

In commerce, plant fibers are broadly defined to include materials that can be spun or twined to make fabrics and cordage, used directly as filling materials, or included in paper production. Plant fibers of commerce are

MAJOR FIBER PLANTS AND THEIR USES

Common Name	Scientific Name	Fiber	Family	Native Region	Uses
Flax	*Linum usitatissimum*	Bast (stem)	Linaceae	Eurasia	Linen fabrics, seed oil
Ramie	*Boehmeria nivea*	Bast (stem)	Urticaceae	Tropical Asia	Textiles (blended with cotton), paper, cordage
Hemp	*Cannabis sativa*	Bast (stem)	Cannabaceae	Eurasia	Cordage, nets, paper
Jute	*Corchorus capsularis, Corchorus olitorius*	Bast (stem)	Tiliaceae	Eurasia	Cordage, burlap bagging
Kenaf Roselle	*Hibiscus cannabinus* *Hibiscus sabdariffa*	Bast (stem)	Malvaceae	Africa, India	Paper, cordage, bagging, seed oil
Sunnhemp	*Crotalaria juncea*	Bast (stem)	Fabaceae	Central Asia	Cordage, high-grade paper, fire hoses, sandals
Urena	*Urena lobata, Urena sinuata*	Bast (stem)	Malvaceae	China	Paper, bagging, cordage, upholstery
Sisal Henequen	*Agave sisalana* *Agave fourcroydes*	Hard (leaf)	Agavaceae	Mexico	Cordage, bagging, coarse fabrics
Abacá	*Musa textilis*	Hard (leaf)	Musaceae	Philippines	Marine cordage, paper, mats
Upland cotton	*Gossypium hirsutum*	Seed trichome	Malvaceae	Central America	Textiles, paper, seed oil
Sea Island cotton	*Gossypium barbadense*			South America	
Tree cotton	*Gossypium arboreum, Gossypium herbaceum*			Africa	
Kapok	*Ceiba pentandra*	Fruit trichome	Bombacaceae	Pantropical	Upholstery padding, flotation devices
Coir	*Cocos nucifera*	Fruit fiber	Aracaceae	Pantropical	Rugs, mats, brushes

classified by the part of the plant from which they are obtained: (1) stem or bast fibers of dicotyledonous plants arise from phloem tissues and run the length of the plant between the bark and the phloem; (2) leaf or hard fibers of monocotyledonous plants arise from vascular tissue and run lengthwise along a leaf; and (3) seed or fruit fibers arise from seed hairs, seed pods, or fibrous fruit husks. Other minor sources of plant fibers include entire grass stems and strips of leaves or leaf sheaths from palms.

Bast Fibers. Bast fibers arise from phloem cells in the stems of a variety of dicotyledonous plant species. Fiber cells range from 1 millimeter in jute to more than 250 millimeters in ramie, and individual fibers may be comprised of thousands of cells extending up to 1 meter (3.3 feet) in length. Bast fibers from a number of plant species are employed in the weaving of fine textiles, the manufacture of cordage (rope and twine), and paper production. Bast fibers from flax (*Linum*) are used to make linen, the fabric used in wrapping Egyptian mummies more than four thousand years ago. Fibers from jute (*Corchorus*) have been used since biblical times, and it remains the world's most important source of bast fibers, yielding twice as much fiber as all other sources combined. Coarse cloths, rope, and twine are produced from hemp (*Cannabis*), ramie (*Boehmeria*), and sunnhemp (*Crotalaria*), while bast fibers from a number of plants such as hemp, sunnhemp, and *Urena* are important in paper production.

Bast fibers are localized inside the stem and are cemented to adjacent cells with pectins (a form of carbohydrate). Because of this intimate association, bast fibers are isolated from surrounding tissues using a combination of processes that incorporate bacterial decomposition (called retting), mechanical separation of fiber from wood and bark (scutching), and fine combing to separate individual fiber strands (hackling). In retting, stems are bundled after harvest and allowed to partially decompose in fields, ponds, streams, or tanks. This process of slow decomposition degrades pectins and allows fiber strands to dissociate from adjacent tissues. After retting, the stems are rinsed and dried, and the woody portion of the plant is removed from the fibers by scutching, a process that involves crushing stems in a series of fluted metal rollers. After scutching, bast fibers are hackled by drawing them through sets of progressively finer combs. This separates the long, fine fibers used for spinning and weaving from short fibers that are used in other applications.

Hard Fibers. Hard fibers are obtained from leaves of certain monocotyledonous plants. Individual hard fiber cells range from 1 millimeter in sisal to more than 12 millimeters in abacá. Although individual hard fiber cells are usually shorter than bast fiber cells, fiber strands from abacá can exceed 4.5 meters (15 feet) in length. Hard fibers possess thick, **lignified** secondary cell walls that impart additional stiffness and rigidity to the fibers. Hard fibers find their primary application in cordage, although they are also used in the manufacture of sacks, carpets, and specialty papers. The most important species for hard fibers include sisal (*Agave sisalana*), henequen (*A. fourcroydes*), and abacá or Manila hemp (*Musa textilis*). Sisal and henequen originated in Mexico and have been used extensively since the Mayan era. Present-day uses for sisal and henequen fibers include sacking, cordage, and mats. Abacá fiber comes from the leaves of *Musa textilis*, a member of the banana family. Abacá originates in the Philippines, and its fibers were used to make cloth prior to the arrival of explorer Ferdinand Magellan in 1521. Fibers from abacá are resistant to decay from salt water, making them the preferred source for marine cordage. In addition, abacá fiber is used to make mats, coarse fabrics, and paper stock for currency.

lignified composed of lignin, a tough and resistant plant compound

The extraction of hard fiber from leaves is a simple process, as entire leaves from sisal, henequen, or abacá are fed into a machine called a decorticator, which crushes the stalks and washes away the nonfiber pulp. The resulting ribbons of fiber are then washed and dried and can either be dyed or used directly.

Seed and Fruit Fibers. Only three seed and fruit fibers have commercial importance: cotton, kapok, and coir. Cotton is the most widely used of all fiber plants. Cotton fibers are unicellular hairs (trichomes) that emerge from the seed coat after fertilization. Cotton fibers exhibit two forms: the long "lint" fibers that are twisted into thread and woven into fabrics, and short "fuzz" fibers that are used for batting, felts, and paper production. Single-celled lint fibers grow rapidly and expand approximately 2,500-fold (from 0.020 to 50 millimeters) during maturation. Cultivated for over four thousand years, cotton fiber has historically been obtained from two diploid species (*G. arboreum*, *G. herbaceum*) native to Africa and Asia, and two **tetraploid** species (*G. barbadense*, *G. hirsutum*) native to the Americas. Presently, the tetraploid species account for nearly all of the worldwide production of cotton fiber.

tetraploid having four sets of chromosomes; a form of polyploidy.

Unlike the seed hair of cotton, kapok fibers are produced by the inner surface of fruit pods (capsules) from the silk cotton tree *Ceiba pentandra*. Kapok fibers reach 20 millimeters in length at maturity, and are waxier and one-sixth the weight of cotton fibers. These properties make kapok difficult to spin; however, its water resistance, light weight, and resilience make kapok an excellent waterproof material for upholstery and life-preservers. Coir fiber is made from the husk (mesocarp) of fruits from the coconut palm *Cocos* *nucifera.* To produce coir, the husks are retted for up to a year, then beaten to separate individual fibers. The cleaned fibers can be spun into coarse yarns for use in ropes and matting, or for bristles in brushes and brooms. SEE ALSO CANNABIS; COTTON; ECONOMIC IMPORTANCE OF PLANTS; PAPER.

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Flavonoids

compound a substance formed from two or more elements

vascular related to transport of nutrients

gymnosperm a major group of plants that includes the conifers

angiosperm a flowering plant

epidermis outer layer of cells

herbivore an organism that feeds on plant parts

cortical relating to the cortex of a plant

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

Flavonoids are phenolic **compounds** composed of fifteen carbons that are found in land plants, including bryophytes (hornworts, liverworts, mosses) and **vascular** plants (ferns, **gymnosperms**, and **angiosperms**). There are five major types of flavonoids: anthocyanins, flavones, flavonols, isoflavonoids, and proanthocyanidins. They are synthesized in the cytoplasm and subsequently accumulated in small vacuoles that fuse with the central vacuole in both the **epidermis** and cortex. The original function of flavonoids in plant cells is thought to be defensive, providing protection against insect, fungal, and viral attacks and consumption by invertebrate and vertebrate **herbivores**. Over evolutionary time, their functions became diverse. Anthocyanins in floral and vegetative tissues range in colors from yellow to blue. Those found in petals and pollen grains of the flower attract pollinator insects and birds that visit for food. Visibly colorless flavonoids in the epidermal cells, such as flavones and flavonols, serve as ultraviolet shields for the underlying cells. Proanthocyanidins accumulate in vacuoles of **cortical** cells, seed coats, and secondary tissues such as bark, where they form mixtures of brown-black reddish pigments called condensed **tannins** in the walls. Isoflavonoids and flavones are secreted into the surrounding soil layers and function as signals in the interaction between plant roots and nitrogen-fixing bacteria to form nodules. SEE ALSO ANTHOCYANINS; PIGMENTS; VACUOLES.

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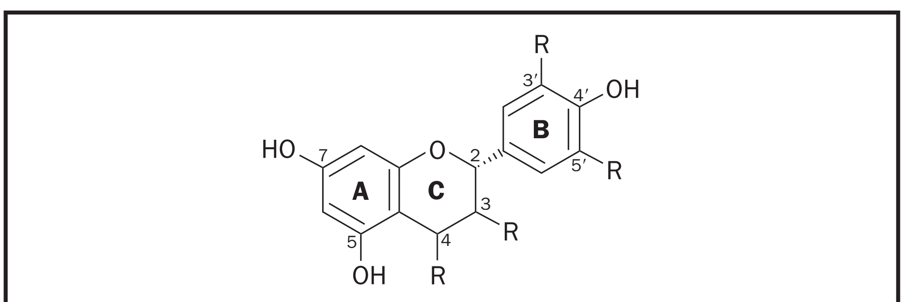

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Flavor and Fragrance Chemist

Flavor and fragrance chemists are professionals engaged in the study and exploitation of materials capable of impacting the human senses of taste or smell. Flavor chemists work primarily with foods, beverages, and food/beverage ingredients; the latter comprise substances that are either derived (directly or indirectly) from plant or animal sources or are chemically synthesized from petrochemicals. Fragrance chemists work mostly with perfumes, fragranced personal care products, and scented household goods and the odoriferous ingredients used therein, which again may include materials of plant, animal, or petrochemical origin.

Research carried out by flavor and fragrance chemists is generally for the purpose of understanding, designing, or improving upon the sensory characteristics of the types of products and ingredients listed above. This often starts with the detailed chemical analysis of a specific target: a finished product or raw materials used in its manufacture. Creative flavorists or perfumers, respectively, with the help of product technologists, may then try to reconstitute flavors or fragrances that match or improve upon the sensory properties of the target. In the case of flavorists, matching a specific natural or processed food or beverage is usually the objective, while a perfumer often has more latitude in cases where the target fine perfume or household air freshener, for example, may be little more than a marketing concept. Product technologists help assure that flavors and fragrances are stable in products and are released and therefore perceivable at the time of consumption or use. Results of chemical analysis may alternatively be used, for example, to design better flavor or fragrance molecules; to make improvements in ingredient formulations or manufacturing processes; or even to provide direction in plant breeding or animal husbandry programs.

Most flavor and fragrance chemists are educated to Bachelor of Science (B.S.) level or higher, often in chemistry, perhaps with specialization in analytical, synthetic, organic, or physical chemistry. In the case of flavor chemists, a degree in food science and nutrition is also common. Additional training is frequently available through professional bodies and industry organizations such as (in the United States) the American Chemical Society, the Institute of Food Technologists, the Flavor and Extract Manufacturers Association, the Research Institute for Fragrance Materials, the Society of Flavor Chemists, and the American Society of Perfumers. Specialized training as a creative flavorist or perfumer, where a highly developed ability to distinguish and describe tastes and odors is absolutely vital, is generally received on the job and involves serving a lengthy apprenticeship.

Employment opportunities in the field of flavor and fragrance chemistry are widespread, especially in North America and Europe, and include university research departments, research institutes, consumer product companies as well as the flavor and fragrance industry. Career opportunities for

Perfumery research chemists from the Roure distillery near Plascassier, France, measure the strength of fragrance given off by roses.

a flavor or fragrance chemist can be extremely varied, including research, flavor/fragrance creation, product technology, quality control, regulatory, and so forth. Accordingly, the work environment is most often laboratory-based but, depending on the nature of the job, can include manufacturing facilities, visits to vendors and customers, and even time spent in remote locations such as African or Amazonian rain forests, searching for sources of novel and interesting flavor and fragrance materials. A career as a flavor/fragrance chemist offers the intriguing challenge of applying state-of-the-art technology to elucidate some of nature's best-kept secrets, involving a fascinating combination of science, creativity, and the use of our senses of taste and smell, in areas we can all readily identify with: namely, the food we enjoy and the odors we encounter on a daily basis. In 1999, salaries ranged from approximately $35,000 at entry level to more than $100,000 for the highly qualified and experienced flavor or fragrance chemist. SEE ALSO Food Scientist; Plant Prospecting.

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Flora

The word flora has two meanings in biology. One definition means all of the vegetation of a region, such as the flora of North America; the other means a book or other work that accounts for all of the plants of a region, such as *The Flora of the Great Plains* or *The Illustrated Flora of North Central Texas.* These books and others like them catalog the plants of a region and include information on distributions and habitat requirements, taxonomic keys for plant identification, and current nomenclature for the plants. The more sumptuous floras also include plant illustrations, distribution maps, and other sources of information. The flora of a region is a dynamic thing, and through time new plants are introduced, old plants change their distributions, some plants go extinct, botanical inaccuracies must be corrected, and new nomenclature must be accounted for. A flora is never truly completed. It is necessary for botanists to revise a regional flora periodically to bring its information up to date.

An illustration from the 1803 edition of *Flora Boreali-Americana,* the first book of American flora that was national in scope.

Systematic botany (or taxonomy) has two notable areas of study. One is monographic (or revisionary) study, with the goal of answering questions about evolutionary relationships, species delimitations, ecological matters, and other issues. The products of these studies are monographs or revisions that are based on field and laboratory studies and that account for a natural group of plants, regardless of where they occur. In the past emphasis was placed on understanding the biological nature of each species, and many research programs incorporated greenhouse and field studies and included studies of **hybridization**, chromosomal variations, and genetic differences associated with the plant's distribution. Such studies (termed *biosystematics*) continue to be important, but the recent past has seen the arrival of sophisticated techniques to analyze the molecular constituents of plant's genetic material, and there has been much effort spent on using molecular taxonomy to show natural relationships, that is, to untangle evolutionary history. The product of monographic or revisionary studies is an authoritative monograph, which reports the results of basic studies on a group of plants. One could say that plants do not come with their names on them. It is the monographer who works out the species and their biologies and puts the proper names on them.

Unlike monographic studies, which are concerned with the biological details of a group of related plants, a flora is concerned with all of the plants of a particular region. Floristicists (or floristicians) must have great field familiarity with their region, and they base their studies on the works of monographers, whose monographs are edited to make their data relevant to the region being studied. For plant groups that have never received monographic study, the flora writer must use his or her intuition as best as possible, based upon experience and the **specimens** at hand. Every floristic botanist can point out plant groups that need further study, either from an imperfect understanding of the plant's biological behavior or from inconsistent information about its ecology and distribution. Even though the knowledge of the plants in a region may be incomplete, there is still a need to communicate what is known to the other scientists in the field, who need to have accepted names for plants in hand, a means of identification for them, and readily accessible ecological information.

hybridization formation of a new individual from parents of different species or varieties

specimen object or organism under consideration

Systematic botanists sometimes speak of the "cascade" of botanical information, whereby the monographers do basic studies on natural plant groups. The writers of floras then synthesize these studies into books that are passed to the primary consumers of botanical information, such as applied scientists, including agronomists, foresters, environmentalists, land managers, and others. From these people, the information flows on to the ultimate consumers: farmers and ranchers, business and industrial people, and, finally, householders. SEE ALSO BIOGEOGRAPHY; HERBARIA; IDENTIFICATION OF PLANTS; SYSTEMATICS; TAXONOMIC KEYS; TAXONOMY.

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Flowers

An enormous diversity of size, shape, and complexity exists among the flowers of the quarter-million species of **angiosperms**. Flower size varies over a thousandfold, with *Rafflesia* (Rafflesiaceae) flowers as large as 1 meter in diameter dwarfing the minuscule flowers of *Wolffia* (Lemnaceae), which measure less than 1 millimeter across. The number of floral organs also varies, with the complex flowers of the *Tambourissa* (Monimiaceae) species having more than one thousand organs while the simple flowers of the Chloranthaceae may consist of just a few. The coevolution of angiosperms with their animal pollinators is a driving force in the generation of flower diversity. The end product of pollination is the formation of a **viable** seed, therefore ensuring that the species will be perpetuated. Exclusive pollinator-flower relationships ensure that pollen will not be wasted by delivery to flowers of a different species.

angiosperm a flowering plant

viable able to live or to function

Definition and Flower Parts

Despite the enormous diversity in the number, size, and shape of floral organs within the angiosperms, they all are built of four basic organ types (**sepals**, petals, stamens, and **carpels**) whose relative positions are invariant. The flower is an assemblage of **sterile** and fertile (reproductive) parts borne on a shoot or axis called the receptacle. The sterile parts include the sepals (collectively called the calyx) and the petals (collectively called the corolla). The sepals and petals together constitute the perianth. In a typical flower the sepals are green, and they enclose and protect the young flower before it opens. The petals, whose function is to attract pollinators, exhibit an assortment of colors, shapes, and sizes. In flowers in which the sepals and petals are indistinguishable from each other, such as tulips (Liliaceae), the perianth parts are called **tepals**.

The reproductive parts can be divided into the androecium and **gynoecium**. The androecium is composed of stamens, the male floral organs. Stamens usually have an apical anther, in which pollen develops, and a basal **filament** connecting the anther to the receptacle. One or more carpels constitute the gynoecium. Carpels are made of several functional tissues that facilitate pollination and protect developing ovules and seeds. The stigma on which the pollen germinates, and the style, through which the pollen tube grows toward the ovules, are examples of tissues that are intimately associated with pollination. The ovary, which houses the ovules, provides protection for both the developing ovules and seeds. In addition, the ovary often develops into a fruit that facilitates seed dispersal. The formation of a protected chamber in which the ovules and seeds develop is one of the defining features of angiosperms. The term angiosperm is derived from the Greek *angio* (a capsule-like covering) and *sperm* (seed).

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

sterile non-reproductive

tepal an undifferentiated sepal or petal

gynoecium the female reproductive organs as a whole

filament a threadlike extension

MAJOR ANIMAL POLLINATORS AND TARGETED FLOWERS

Animal	Flower Characteristics
Beetle	Open flower, white or dull coloring with strong odor (usually fruity, spicy, or similar to the foul odors of fermentation).
Bee	Any color but red; flower has nectar at the base of the flower that forces the bee to pass by the stigma and anthers on its way to the nectar.
Butterfly and some moths	Flowers tubular in shape, which precludes large insects from crawling into them but allows the long proboscis of the butterfly or moth to enter. Nectar contains amino acids that butterflies require; nectar is their sole food source.
Bird	Usually bright and showy flowers, the colors of which are red, orange, or yellow. Because of the bird's high rate of metabolism, bird-pollinated flowers usually produce large quantities of thin nectar. In the Western Hemisphere hummingbirds are the main bird pollinator; in other parts of the world representatives of other specialized bird families (e.g., sunbirds and honeyeaters) act as pollinators.
Bat	Large white flowers such as those of the saguaro cactus (Cactaceae), which are visible in dim light. Bats also require large amounts of nectar.

Function of Flowers

The function of the flower is to facilitate the reproduction of the organism. Cells within the pollen and embryo sac are **haploid** and are derived from the **diploid** cells that develop within the anthers and ovules, respectively. In angiosperms, pollination results in double fertilization. The egg cell nucleus fuses with a sperm nucleus to produce the zygote while the other sperm cell nucleus fuses with the two polar nuclei to form the triploid **endosperm**. The endosperm acts as a food supply for the developing embryo. After fertilization, the ovule with the developing embryo becomes a seed and the ovary becomes the fruit that houses the seed(s).

haploid having one set of chromosomes, versus having two (diploid)

diploid having two sets of chromosomes, versus having one (haploid)

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

Diversity of Flowers

Among the quarter-million species of angiosperms, there are many variations of the generalized flower yielding an immense diversity of floral patterns. The diversity is due to variations in the number, symmetry, size, and fusion of floral parts. While most flowers contain both stamens and carpels (and are referred to as hermaphroditic), other flowers are unisexual. These may be either staminate flowers (missing the carpels) or carpellate flowers (missing the stamens). Species bearing both carpellate and staminate flowers on a single plant are referred to as monoecious ("one house"; maize [Gramineae] and oak trees [Fagaceae], for example). In contrast, dioecious ("two houses") species bear staminate and carpellate flowers on different plants (willow [Salicaceae], for example). Monoecism and dioecism, both of which have evolved multiple times within the angiosperms, provide a mechanism to promote outbreeding. Many other species have evolved more subtle mechanisms to promote cross-pollination. For example, plants may be self-incompatible; that is, they discriminate between self and nonself pollen and consequently reject their own pollen. Alternatively, a difference in the timing of maturation of the androecium and gynoecium in hermaphroditic flowers favors outbreeding.

Two conspicuous characters that contribute to floral diversity are the number and size of floral organs. Angiosperms are often divided into two groups based on their cotyledon number: monocotyledons (monocots, meaning one cotyledon) and dicotyledons (dicots, meaning two cotyledons). One of the characters that distinguish monocots from dicots is the

A bleeding heart flower. Angiosperms, with a quarter-million species, display an enormous variety of flowers.

appendages parts that are attached to a central stalk or axis

whorl a ring

number of **appendages** within a **whorl**. Monocots usually have flowers with floral parts in multiples of three, whereas the dicots often have floral parts in multiples of four or five. Organ size can also vary enormously. For example, in the species *Lepidium* (Brassicaeae), the petals are microscopic, but in the genus *Camellia* (Theaceae), some species have petals 15 centimeters long.

Variations in fusion, arrangement, and symmetry of floral organs provide further diversity. Fusion between organs of the same whorl (coalescence) and fusion of organs from separate whorls (adnation) is common among many families of angiosperms. For instance, coalescence is seen in snapdragon (*Antirrhinum*, Scrophulariaceae) with the petals fused at the base, and adnation in tobacco (*Nicotiana*, Solanaceae) with stamens fused to the petals. Position of organ attachment to the receptacle also influences flower architecture. If the corolla and stamens attach to the receptacle below the ovary, the flower is referred to as having a superior ovary (e.g., *Liriodendron tulipifera*, Magnoliaceae). In contrast, having the corolla and stamens attach to the receptacle above the ovary produces a flower with an inferior ovary (e.g., *Iris*, Iridaceae). In radially symmetric flowers, termed actinomorphic, all organs within any particular whorl are identical and positioned equidistant from other organs within the whorl (e.g., California poppy *Eschscholzia californica*, Papaveraceae). Flowers in which organs in a particular whorl differ from other organs in the same whorl are referred to as zygomorphic (e.g., most orchids, Orchidaceae).

pheromone a chemical released by one organism to influence the behavior of another

While all of the mechanisms generating diversity contribute to their interactions with pollinators, the fusion and asymmetry of floral organs has allowed the evolution of fascinating and often bizarre plant-insect interactions. For example, some species of orchids attract potential pollinators with insect **pheromones**, luring the insect into a maze constructed of fused petals and stamens in which there is one entrance and one exit. In navigating the maze, the insect both delivers to the stigma of the gynoecium pollen from another flower and picks up a load of pollen to be distributed to another flower.

Evolution of Flowers

While angiosperms are prevalent in the fossil record from the mid-Cretaceous (approximately one hundred million years ago), it is thought that they may have evolved substantially earlier, perhaps as far back as two hundred million years ago. The closest extant relatives of the angiosperms are the gymnosperms, of which conifers are members. Conifers do not have flowers but rather produce female and male cones consisting of scales bearing exposed ovules and pollen sacs, respectively. It's intriguing to consider what evolutionary processes occurred to produce the complex assemblage of floral organs of extant angiosperms. Charles Darwin, upon thinking about this question, stated that flowers are an "abominable mystery." The answer to this question, however, may be found in comparative genetic studies. For example, some of the important regulatory genes promoting floral organ development are also found in conifers. Understanding their function in the cones of conifers may allow scientists to model evolutionary changes that occurred resulting in the formation of early flowers.

It is not clear which features were present in the flowers of the earliest angiosperms. Although by the mid-Cretaceous period angiosperm flowers were already quite diverse, a number of key features of extant flowers had not yet appeared. Fossil flowers from the Cretaceous often have organs that are spirally arranged, a perianth that does not have a distinct calyx and corolla, relatively few stamens, and multiple carpels that are not fused together. The attractiveness of the mainly fly- and beetle-pollinated flowers was due to the androceium, which was composed of anthers attached to showy, leaflike structures. The stigma and style of the early individually fused carpels ran down along the side of the ovary instead of being at the top, as seen in most extant carpels.

There are a number of major evolutionary trends when comparing these Cretaceous flowers to their modern counterparts. For example, in many modern flowers the perianth is differentiated into a distinct calyx and corolla. The evolution of the corolla facilitated the reduction in stature of the androecium such that the stamens are composed of anthers attached to slender filaments rather than large, leaflike appendages. In addition, fusion of organs occurred along with the establishment of zygomorphic flowers, creating flowers with deep, open, funnel-shaped flowers, both innovations allowing the evolution of elaborate pollination strategies. Another evolutionary trend is the formation of a gynoecium made up of multiple fused carpels that have only one stigma and style situated at the apical end of the ovary. This has been hypothesized to provide selection at the level of the male **gametophyte**, which must grow through these structures to effect fertilization.

gametophyte the haploid organism in the life cycle

Coevolution with Pollinators

The early seed-producing plants (such as conifers) utilize wind to move pollen from the staminate cones to the female ovule-bearing cones. To ensure that enough viable seeds are generated, copious quantities of pollen need to be produced. This process requires the expenditure of large amounts of stored resources and is not very efficient. Utilizing insects to transfer pollen to other flowers enables angiosperms to produce less pollen and still maintain a high fecundity in comparison with wind-pollinated plants. In contrast to flowers of early angiosperms, extant flowers have evolved highly attractive characters to ensure that a specific pollinator continues to visit flowers from a specific species of plant. Flowers provide special sources of food for their pollinators to induce them to visit similar flowers. In addition to pollen and other edible floral parts, nectaries provide nectar, a high-energy food source for animals that can sometimes contain amino acids, proteins, lipids, **antioxidants**, and alkaloids.

antioxidant a substance that prevents damage from oxygen or other reactive substances

Many of the modifications that have evolved in angiosperm flowers are adaptations to promote constancy in pollinator visitation. However, not all angiosperm flowers require animal pollinators. The grasses, which evolved from insect-pollinated flowers, are wind-pollinated. The flowers of grasses are small with reduced or absent petals, and they produce large amounts of pollen.

The Development of Flowers

A basic floral ground plan exists that defines the relationship between organ type and position in all angiosperm species. Because of the constancy in the relative positions of floral organ types, it is hypothesized that a common genetic program to specify floral organ identity is utilized during the development of all flowers. Floral organs are ultimately derived from **primordia** that arise from the flanks of the flower **meristem**. It is thought that cells within the flower meristem assess their position relative to other cells and differentiate into the appropriate floral organ based on this positional information.

primordia the earliest and most primitive form

meristem the growing tip of a plant

To clarify how the identity of flower organ primordia is specified, researchers have taken a genetic approach. Mutations affecting flowers and their organs provide a powerful means for studying the genetic interactions involved in their development. Differences in the development of mutant versus normal (wild-type) plants reveal the function of the mutated gene. To carry out this work, researchers use two model plant systems, *Arabidopsis* (Brassicaceae) and *Antirrhinum* (Scrophulariaceae), and screen plants that have induced mutations in their **genome**. Studies have focused on a particular set of **homeotic** mutations. In homeotic mutants, normal organs develop in the positions where organs of another type are typically found. Specifically, the *Arabidopsis* floral homeotic mutations result in transformations of one floral organ type into another floral organ type.

genome the genetic material of an organism

homeotic relating to or being a gene producing a shift in structural development

It is of interest to note that several homeotic mutants exist in commonly cultivated garden plants. For example, a wild rose flower has five petals, and yet some of the hybrid tea roses have many times that number. Similar situations exist for camellias and carnations. These **hybrid** varieties represent changes in the genetic constitution of the plant to yield alterations in the floral architecture, which some people find attractive. SEE ALSO ANGIOSPERMS; GENETIC MECHANISMS AND DEVELOPMENT; IDENTIFICATION OF PLANTS; INFLORESCENCE; INTERACTIONS, PLANT-INSECT; POLLINATION BIOLOGY.

hybrid a mix of two species

Stuart F. Baum and John L. Bowman

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Food Scientist

A food scientist studies the science and technology of production, manufacturing, processing, product development, packaging, preparation, evaluation, distribution, utilization, and safety of food products. A food scientist can work and study in a wide range of areas, from meat science to dairy science to the science of fruit and vegetable products.

Food science plays a critical role in the health, welfare, and economic status of all individuals and nations. The food industry is one of the largest manufacturing industries in the United States, employing over two million people, with an additional fifteen million employed in other food-related fields and contributing more than $350 billion to the gross national product.

A food scientist must have an understanding of the basic sciences, which can include chemistry, biochemistry, biology, microbiology, toxicology, nutrition, engineering, marketing, economics, math, and physics. The scientist applies the principles of these basic sciences and engineering to the study of the physical, chemical, and biochemical nature of foods and food processing.

A food scientist tests samples of wine in a German laboratory.

A food scientist with a specific interest in products of plant origin works primarily with fruit, vegetable, cereal grain, and oilseed products. In this work, the individual is concerned with the impacts of preharvest, postharvest, processing, and preservation variables and practices on the yield and quality of the processed product. For instance, a food scientist might monitor the impact of storage temperature on vitamin levels in wheat or the effect of a new oil extraction process on the shelf life of sunflower oil.

Degrees available to individuals desiring to study the food sciences include a Bachelor of Science (B.S.), a Master of Science (M.S.), and a Doctor of Philosophy (Ph.D.). A bachelor's degree in food science would qualify the individual for employment in such positions as a food processing production line supervisor; a laboratory technician with an industry, government, or independent research organization; or as a regulatory supervisor with a state or federal agency. With a master's degree, the food scientist would be eligible for positions such as quality control manager, process control supervisor, product development coordinator, or business manager. A doctoral degree would allow the individual to work in the areas of education, research, and outreach either with a university system, state or federal agency, or within the food science/food processing industry. The food industry is rapidly growing as population increases and with increasing demands for convenient, safe, and nutritious foods and beverages. The growth of the industry and its need for professionals make it possible to find a wide variety of careers.

The work environment for graduates in this career can be highly variable, ranging from outdoor fieldwork, including food production and raw product quality control, to processing plants, research laboratories, and classrooms. Employment is available in all fifty states and opportunities are available in basically all foreign countries. Because of the need for food scientists, salaries are often equal to or higher than those of other professions requiring equivalent levels of education. In 1999, food scientists with a bachelor's degree could expect a starting salary of $30,000 to $40,000. A master's degree earned a starting salary of $35,000 to $45,000, and a doctorate started at $50,000 or higher. SEE ALSO Agronomist; Alcoholic Beverage Industry; Flavor and Fragrance Chemist; Oils, Plant-Derived.

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Forensic Botany

Forensic botany is the application of the plant sciences to legal matters. Most often this means using clues from plants in order to aid in the solution of serious crimes such as murder, kidnapping, and the cause of death of a victim. Many aspects of plant science are employed, including plant anatomy, the study of plants cells; plant taxonomy, which deals with the identification of plants; plant systematics, focusing on plant relationships to other plants; plant ecology, which deals with plants and their environments; and palynology, which is the scientific study of plant pollen and spores.

Plant cells possess cell walls made of cellulose, a complex carbohydrate **compound** that is virtually indestructible in comparison with most other natural compounds subject to decay. Plant cell walls can remain intact for thousands of years even though the cytoplasm long since has disappeared. The walls around pollen grains and spores also are made of different materials that are also resistant to decay. This allows plant parts to remain identifiable for long periods of time.

compound a substance formed from two or more elements

The plant foods we consume have distinctive cells within them. The tissues of food plants are made up of cells of distinctive shapes and sizes that are arranged in distinctive patterns. These characteristics are preserved all the way through the human digestive tract and beyond. This also is true for wood. This means it is possible to tell what a person's last meal was long after death. Also, if a person was stuck with a piece of wood, that piece often can be identified to species and/or matched to the larger wood piece from which it was obtained. Sometimes seeds, leaves, and plant fragments are associated with a crime. If the plant can be identified from these clues by a plant taxonomist, they may link the crime to a specific place (for example, one associated with a suspect). Also, taxonomists can be called upon to identify drug plants that are illegal in this country, such as coca.

Plant ecology has been found useful in the location of the graves of missing persons. It does not matter whether the grave is deep or shallow or whether the person was clothed, encased in plastic, or naked at the time of burial. The clues for the burial site come from the necessity of disturbing vegetation cover to dig a grave. A knowledge of plant **succession** patterns in the area is almost impossible to disguise from the eyes of a well-trained plant ecologist. They remain evident for at least a few years, and sometimes for a decade or more.

succession the pattern of changes in plant species that occurs after a soil disturbance

Palynological evidence can be used to suggest where a person was killed and to link a suspect to a crime scene. It also can be used to identify controlled (illegal) plant substances even if no other plant material is present.

Forensic botany is a new and growing field. Many criminal investigators, medical examiners, and attorneys are unaware of its usefulness because they have had little exposure to botany in their educational experiences. Most forensic botanists act as private consultants in crime matters. To be accepted to testify in a court case, forensic botanists must demonstrate that they are qualified to be expert witnesses. Their suitability for such testimony is judged by their experiences and educational credentials. SEE ALSO PALYNOLOGY; PLANT COMMUNITY PROCESSES.

Jane H. Bock and David O. Norris

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A forester with the Union Camp Corporation grafts a young pine bud onto an older plant that will someday be used for the manufacture of forest products.

Forester

Foresters practice and promote the art, science, technology, and profession of forestry. The field of forestry encompasses a diverse group of people working in many different areas. Foresters can be found in the woods, lumber mills, laboratories, classrooms, offices, urban areas, and even Congress.

The role of a forester can vary greatly, from technicians who focus mainly on forest inventory and management to urban foresters who focus on tree care in the urban setting. Other forestry jobs include consultants, who provide services to private landowners on how best to manage their lands to meet their objectives; rangers, who manage federal park and forest lands to meet specified goals; and professors, who teach the art, science, and technology of forestry. Foresters may also be nurserymen who produce tree seedlings; firefighters who work to extinguish uncontrolled forest fires; or lobbyists who provide vital forest-related information to policymakers, congressmen, and the public.

To become a professional forester, one must obtain a college degree from a school offering professional forestry education. Degrees include a two-year associate's degree, which qualifies the graduate to work as a forest technician, or a four-year bachelor's degree, after which the graduate typically starts in an entry-level position with the opportunity to advance to managerial positions. Graduates earning a master's or doctoral degree tend to focus on highly specialized areas of forestry, working as researchers, geneticists, and professors.

Foresters work in very diverse areas under varied conditions. From the old-growth forests in the northwest to the pine plantations in the southeast, foresters work hard to ensure that the land is managed properly. Foresters are also found in other parts of the world, such as Australia, Africa, Germany, Canada, and many other places.

From friendship to travel, the benefits of becoming a forester are numerous. The responsibility of quality land management rests in the hands of foresters, who take pride in the fact that they have the ability and scientific knowledge to improve forest health and productivity. Having fun is another great benefit of becoming a forester. Of all the rewards, though, one of the greatest may be found in teaching others about this great field. According to the *Occupational Outlook Handbook*, published by the Bureau of Labor Statistics and the U.S. Department of Labor, forester salaries ranged from $19,500 to $62,000 in 1997.

The job of a forester can encompass many different kinds of work. However, all foresters share one thing: the responsibility of managing a natural, renewable resource. Foresters take this job seriously and respect what the land has to offer, for it is the lifeblood of the profession. Without foresters and the science of forestry, forests would not be as healthy and productive as they are today. When you become a forester, you make a difference for generations to come. SEE ALSO CONIFEROUS FORESTS; DECIDUOUS FORESTS; RAIN FORESTS; TREES; WOOD PRODUCTS.

Sunburst Shell Crockett

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Forestry

Forestry is the discipline embracing the science, art, and practice of creating, managing, using, and conserving forests and associated wildlife, water, and other resources for human benefit and in a sustainable manner to meet desired goals, needs, and values. The broad field of forestry consists of those biological, quantitative, managerial, and social sciences that are applied to forest management and conservation. Forestry includes specialized fields, such as tree nursery management, forest genetics, forest soil science, silviculture (manipulating and tending forest stands), forest economics, forest engineering, and agroforestry (growing trees and food crops on the same land). Industrial forestry is focused on efficient and profitable production of trees for wood or fiber while meeting criteria of water and air quality, wildlife habitat, and esthetic values. In Oregon, Washington, California, and other states there are regulations governing forest management practices. Nonindustrial forestry (or small, private forestry) is practiced by many landowners to provide wood for income, recreational, and esthetic values and, often, a forest retreat from the bustle of urban life. Multiple-use forestry, practiced on many federal lands in the United States, includes considerations of potential wood

A logging camp on Okanagan Lake in British Columbia.

production, wildlife habitats, recreation opportunities, watershed protection, grazing opportunities for cattle or sheep, and special values such as nests of rare birds or areas of historical or spiritual significance. Wilderness and recreation areas of federal and state forest lands are managed with special considerations for maintaining pristine landscapes and providing opportunities for hiking, camping, boating, and other activities compatible with forests.

Foresters use a broad variety of technical skills, techniques, and equipment to tend, manipulate, and harvest forest trees and to evaluate and maintain water, wildlife habitat, recreation, and scenic values of forests. Foresters measure and evaluate resource values using aerial photographs, satellite images, global positioning systems, laser measuring devices, statistical sampling systems, field computers for data entry, and computer systems for data compilation, calculations, and simulation modeling (e.g., FORTOON, a gaming simulation by J. P. Kimmins of the University of British Columbia and associates). In harvesting trees and planning the next forest, foresters are concerned about tree sizes and the strength qualities of wood, disturbances to the remaining forest that may affect planting new trees, and maintaining water quality and wildlife habitat values. Regenerating a new forest, which may be expected to grow for twenty to one hundred or more years (depending on forest type and tree species), often involves planting seedlings, small trees grown in nurseries or greenhouses. These seedlings may be genetically improved, that is, grown from seeds from carefully selected and tended parent trees. New seedlings must often be protected from being eaten by deer, mice, or other forest dwellers, and competing vegetation (like weeds in a garden) must be controlled so the new trees can grow. Where the land is not too hilly or steep, trees can be planted from a plowlike machine pulled behind a tractor. In mountainous areas workers plant trees by hand using special hoes or shovels. In some forests, especially those of pines and other conifers, foresters often thin out some trees after a few years to leave more growing space for desired trees. And, on certain types of soils that are not so fertile, foresters may add fertilizers to improve tree growth (just as one might fertilize a lawn or garden).

Planning and management of forests must include consideration of the following matters:

- What kinds and amounts of wood can be cut, removed, and sold?
- Should all trees be cut (clearcut), only a few high-value trees (selection harvest) be cut, or should most trees be removed, leaving a few for shade and seed for the next forest (shelterwood)?
- What parts of a forest should or must be protected for the common good (e.g., streams and streamside zones; critical wildlife habitats, such as eagle nests; areas of special scenic beauty)?
- What can be kept as trees are cut (e.g., campsites; hiking trails; scenic vistas)?
- Operations planning: for instance, road building, timber harvest and transport, reforestation; forest stand tending (control of competing vegetation; thinning)
- Financial analysis: for instance, assessing where wood can be sold; costs, expenses, and potential profits; reinvestments needed for things such as road maintenance, tree nurseries, and pest controls.

For many state and all federal forest lands, and increasingly for private industrial forests, planning and management activities must involve informing neighbors and others of how the forest, including water, wildlife habitats, and recreation values will be changed. People care about *their* forests, whether they own them or not.

Forest scientists at universities and industrial, state, and federal research sites are constantly involved in seeking knowledge about how natural forests grow and change and how to grow better trees for human use. Today this research includes genetic engineering research with trees. An example of this is production of a tree that will not be killed by a weed-killing chemical (herbicide) used to control plants competing with desired tree growth. Research continues on basic wood structure and how to get more trees with desired wood strength or whiter paper-making fibers. Foresters and forest scientists are very knowledgeable about many aspects of how forests grow and change. But with increasing replacement of natural forests by managed plantations, and with urban areas expanding to forest edges, more detailed knowledge is needed about how trees use water and nutrients and interact with other plants, animals, and microorganisms in forests. Forest ecologists work in laboratories, large-scale research plots, and experimental forests to provide knowledge for better forest management for all forest products and values.

The forests of the world have many types of trees and wood, from black walnut and cherry of the midwest to spruces of the north, pines of the south

Loggers cut samples from a fallen giant sequoia. The tree rings will be studied to discover the sun cycles, amounts of rainfall, climate, and any fire incidences that occurred during the lifetime of the tree.

and Douglas-firs of the Pacific Northwest to eucalyptus trees of Australia. Forest engineers, wood products engineers, and wood scientists work on new ways of harvesting, transporting, and processing trees to make boards, beams, paper, plywood, and glued-together composite materials with very specific properties (e.g., strength), and other products such as the new fabric tencel. These people extend the work of foresters to our homes and everyday lives. SEE ALSO Coniferous Forests; Deciduous Forests; Forester; Rain Forests; Trees; Wood Products.

James R. Boyle

Fruits

angiosperm a flowering plant

pistil the female reproduction organ

The fruit is the mature ovary and its associated parts. This unique covering of the seeds of flowering plants gives this group of plants their name: **angiosperms**. Fruits are formed by the enlargement and maturation of the **pistil**. Common examples of fruits include apples, oranges, grapefruits, lemons, grapes, peaches, plums, cherries, pineapples, and pears. Commonly, when people think about fruits, they think only of the fleshy and flavored fruits. In the botanical sense, however, any flowering plant that produces seeds also produces a fruit that contains the seed. Using the botanical definition, a number of so-called vegetables are actually fruits, including green peppers, tomatoes, cucumbers, squash, beans, and even such grains as corn, rice, and wheat. Fruits may also be hardened, such as walnuts, pecans, acorns, and coconuts. Horticulturalists define fruit crops as those that bear fleshy and flavored fruits. These fruit crops are grown on trees that require years of **cultivation**, but in some plants of the mustard family, the entire life cycle of the plant may be as brief as a month, including fruit formation.

Fruits are formed from the ovary alone in many plants, but in other plants, adjacent tissues that are not part of the pistil may become part of the fruit. These nonpistillate tissues form accessory parts of the fruit. In strawberries, the receptacle, which holds the tiny pistils, forms the fleshy part of the fruit. Pears and apples are two related examples of fruits formed by a floral cup located next to the ovary.

Cross section of a Chardonnay grape.

Function

The function of the fruit in flowering plants is to protect the seeds and to facilitate their dispersal. Fleshy fruits are usually edible and are dispersed after being eaten. Color changes in fruit often signal ripeness and make ripe fruit easy to see. When fruits are eaten, the seeds pass through the gut mostly unaffected. In fact, in some cases, the partial breakdown of the seed coat stimulates germination. Excreted seeds are surrounded by nutrients (including minerals and simple organic **compounds** in the dung) along with a **substrate** for early growth. Of course, this strategy fails if the seeds are actually digested. As a plant defense mechanism, some plants produce chemicals that can make an animal ill if too many are digested. Some of the plants modified by man no longer have such chemical defenses.

cultivation growth of crop plants, or turning the soil for this purpose

compound a substance formed from two or more elements

substrate the physical structure to which an organism attaches

Dry fruits are characteristic of seeds dispersed by the wind and other natural agents or animals. These fruits may have barbs, hooks, or a sticky surface that catches the coat of a passing animal and disperses the seeds. Winged fruits or those with tufts of hair are designed to catch the wind (for example, dandelions). Fruits of seaside plants often float and are resistant to water damage. The occurrence of coconut palms on seashores around the world is evidence of the success of this strategy. A fibrous husk traps air and conveys the hard seed to the high-water mark on a beach where the plant can become established. Some plants, particularly those of the California chapparal, thrive after fire. Fire-adapted fruits not only withstand fire temperatures, but may need them to trigger seed release.

Dry fruits often have specific adaptations for seed release. Many dry fruits are dehiscent, forming openings at specific locations in the wall. How the fruit opens determines whether seed release occurs slowly or all at once. Some dry fruits are indehiscent and do not open at all prior to seed germination.

Fruit Development and Ripening

The formation of fruits is typically triggered by sexual fertilization. Many changes occur in the flower accompanying fertilization, including the loss of petals, anthers, and stigma, modification or shedding of the **sepals**, development of the ovules into seeds, and formation of the embryo and **endosperm** within the seed. As part of fruit formation, the walls of the ovary surrounding the seeds are stimulated to resume cell division and to expand. The differences in the size and shapes of fruits are limited to some extent by the structure of the flower, and to an even larger degree by later patterns of growth.

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

Some fruits do not form seeds, such as bananas and seedless grapes. Fruits produced without seeds are examples of so-called parthenocarpic fruits, in which ovules (precursors of seeds) are formed but do not successfully fertilize.

stimulus trigger

Plant hormones play an important role in the formation and maturation of fruit. Fleshy fruits grow and thicken in response to hormonal growth signals emitted by fertilized seeds. In strawberries, for example, seed formation is highly successful except for the tip of the fruit, which is poorly developed. Where seeds are underdeveloped, so is the fruit. The **stimulus** for fruit production in this plant can be replaced by a plant hormone known as auxin, which is often produced by developing seeds. Fruit maturation and the development of fruit color are triggered by a later-occurring hormonal signal, produced by the gas ethylene. For grocery stores, fruit is often picked before becoming ripe because unripe fruit is not as easily bruised. To ripen the fruits for sale, a human-made gas related to ethylene is used after harvest, causing the immature fruit to develop its characteristic color and texture.

Once the fruit is ripe, the pedicel or stem that holds the fruit begins to seal itself off from the plant, under the influence of the hormone abscisic acid (ABA). When this hormone is produced, fruit drop is stimulated. To prevent fruit drop, another hormone called cytokinin can be used to inhibit the production of ABA and delay overripening and fruit drop. Oranges and other citrus crops can be harvested yearlong by inhibiting fruit drop and senescence through the application of a cytokinin. Citrus fruits, which normally mature in the winter, can thus be harvested year round.

A careful examination of the fruit reveals how the tissues change during development. In citrus fruits, like grapefruits and oranges, the bulk of the fleshy fruit is formed by small juice sacs, which originate from small hairs lining the inside of the pistil. These juice sacs are simply hairs that swell at different positions along their length, filling the fruit. The nature of these hairs can be seen by gently teasing a few sacs from the center of the fruit. The fleshiness of the tomato fruit is the result of the swelling of the placenta, a tissue that connects the seeds to the walls. Frequently, the ovary wall itself forms most of the fruit, but the exact region of thickening differs in each plant group. In squash, cucumbers, and pumpkins for example, the middle of the ovary wall grows thicker than the inner and outer layers, whereas in grapes, the inner wall grows thicker, and in watermelons, the outer wall is particularly thick. In dry fruits, the thickening of the ovary wall is sometimes accompanied by cell hardening, which is caused by chemical changes in the cell walls. These hardened cells form the walls of nuts and other hard fruits. In dry fruits, the walls of the fruit are no longer living.

Types of Fruits

Fruits consist of three major types, depending on whether they are formed from a single flower with fused or unfused multiple simple pistils or from multiple flowers: (1) simple fruits consist of one simple or fused pistil, in which the pistil forms the simple fruit; (2) aggregate fruits consist of many unfused pistils as part of a single flower; and (3) multiple fruits consist of many flowers on the same floral stem fusing together during growth. Fruits formed with large areas of nonpistillate parts in the flower are known as accessory fruits, a term that may be used in combination with these other terms.

FRUIT CATEGORIES AND COMMON EXAMPLES

Major and Minor Categories of Fruit Types				Common Examples
Simple fruits (develop from one pistil and often include surrounding [accessory] ovary tissues)	**Fleshy fruits**	**Berry** (multi-seeded fruits with rind or skin-like covering)	**Typical berry** (fruits with skinlike covering)	Grape, tomato, gooseberry, cranberry
			Pepo (fruits with inseparable rind)	Cucumber, pumpkin, squash
			Hesperidium (fruits with separable rind)	Orange, grapefruit, lemon
		Drupe (single seeded with thin skin)		Peach, plum, cherry, olive
		Pome (multi-seeded fruit formed from floral tube [inferior ovary])		Apple, pear, quince
	Dry fruits	**Dehiscent fruits** (fruits that split at maturity)	**Legume** (single pistil forming two slits)	Peas, beans, locust
			Follicle (single pistil forming a single slit)	Milkweed, columbine, larkspur, magnolia
			Capsule (compound pistil opening variously)	Poppy, purslane, iris, Saint-John's-wort, morning glory
		Nondehiscent fruits (fruits that do not naturally split at maturity)	**Grain** (caryopsis; one-seeded with inseparable covering)	Corn, wheat, oats, rye, barley
			Achene (one-seeded with separable covering)	Sunflower, lettuce, buckwheat
			Samara (winged achene)	Ash, maple, elm, birch
			Nut (one-seeded, hard covered fruit with large embryo)	Chestnut, walnut, hazelnut, acorn, beechnut
Aggregate fruits (develop from one flower with multiple separate pistils)				Strawberry, raspberry, blackberry
Multiple fruits (develop from a flower cluster, multiple flowers of an inflorescence)				Pineapple, mulberry, osage orange, fig

Simple fleshy fruits are divided into three major types. Berries are multi-seeded fruits covered by a thinner skin (as in tomatoes) or a thickened rind (as in cucumbers). Some berries may be further divided into subtypes, including the pepo, characteristic of the cucumber family (e.g., cucumbers, squash, and pumpkins), and the hesperidium, characteristic of the citrus family (e.g., oranges, grapefruits, and lemons). Pomes are also multi-seeded fruits, but their fleshy body consists of largely nonfloral (accessory) parts. Since their body is not just pistil tissue, pomes can be regarded as accessory simple fruits. In pomes, the outer wall develops from the floral cup or hypanthium of the flower, as in apples, pears, and quinces. Drupes are single-seeded fruits that may contain a leathery or stonelike seed. Peaches and plums are examples of fruits with rock-hard seeds at their center, commonly classified as stone fruits.

Simple dry fruits include two types of fruits. Dehiscent dry fruits are those that normally open during the maturation process, releasing their seeds. Frequently, a line of dehiscence forms the opening in the fruit. **Legumes** are formed from single pistils that have two slits or lines of dehiscence on either side of the fruit. Legumes include peanuts and beans, and

legumes beans and other members of the Fabaceae family

are characteristic of the bean family. Follicles are dry fruits, often with vertical slits, which have a single dehiscence line. Capsules are formed from compound pistils and open through a variety of mechanisms. In poppies, these fruits have small pores at the top of their fruits. In contrast, irises form fruits that open along the **suture** lines of the compound pistil, splitting into their component pistils. The position of these openings is used to establish further subtypes (not mentioned here).

suture line of attachment

Nondehiscent dry fruits are those that do not normally open to release their seeds. Four types are commonly found. Grains, or caryopses, are small, one-seeded fruits that have fruit walls that are fused to the seed and are therefore inseparable, as in corn. Achenes are single-seeded indehiscent fruits in which the seed and fruit are readily separated, as in sunflowers. Samaras are winged fruits, such as those of maple, ash, and elm, which are readily dispersed by wind. Nuts are one-seeded fruits as well, but are characterized by their hard covering and often large and meaty embryos, as in walnuts, chestnuts, and acorns.

Aggregate fruits develop from single flowers with multiple separate pistils. Common examples composed mainly of pistillate tissues include raspberry and blackberry. The fleshy region of the strawberry originates from the receptacle of the former flower. Therefore, in addition to being an aggregate fruit, it is also called an accessory fruit.

Multiple fruits consist of the fused flowers of whole inflorescences (or flowering stalks). The most common of the multiple fruits is the pineapple, although the mulberry, Osage orange (or bois d'arc), and fig are also commonly encountered multiple fruits. SEE ALSO FRUITS, SEEDLESS; GRAINS; REPRODUCTION, SEXUAL; ROSACEAE; SEED DISPERSAL; SEEDS.

Scott D. Russell

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Fruits, Seedless

The absence of developed seeds in fruit improves its eating quality. Moreover, it may allow more uniform fruit production in different environments. Seedless fruit occurs when seed (embryo and **endosperm**) growth is inhibited or the seed dies early, while the remainder of the fruit continues to grow. Bananas and grapes are the most commonly available seedless fruits. Bananas are seedless because the parent banana tree is triploid (3X chromosome sets) even though pollination is normal. Generally, species with a chromosome set number divisible by two (e.g., 2X or 4X chromosome sets) are capable of seed production while uneven sets of chromosomes (e.g., 3X or 5X) are either **sterile** or do not produce seeds. After fer-

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

sterile non-reproductive

tilization, banana fruit development can proceed normally but seed development is arrested because of the genetic imbalance. Plant breeders have also produced seedless watermelons (*Citrullus lanatus*). The first practical system for producing seedless watermelons was the 4X-2X hybridization method. **Hybrid** seed is produced from crossing a **tetraploid** (4X) female and **diploid** (2X) male. Seedless fruit is produced on the resulting triploid (3X) hybrids. Pollination occurs, but just as in bananas, the fruit continues to grow while seed growth is reduced or absent because of uneven sets of chromosomes.

hybrid a mix of two varieties or species

tetraploid having four sets of chromosomes; a form of polyploidy

diploid having two sets of chromosomes, versus having one (haploid)

Parthenocarpy, fruit development without pollen fertilization and seed set, can result in seedless fruits such as grapes, squash (*Cucurbita pepo*), and eggplants (*Solanum melongena*). The majority of table grapes and raisins are seedless. Thompson seedless grapes have a normal chromosome constitution and pollination but have specific genes causing seedlessness. In addition, seedless grapes are treated with the hormone gibberellin, which is applied early in fruit development. The application of this hormone increases the size and consistency of the fruit.

Squash and eggplants can exhibit **facultative** parthenocarpy, that is, parthenocarpy that occurs under environmental conditions where pollination and seed would not occur normally. Cool weather (early spring or late fall) or greenhouse growth conditions are the most common environments where this type of parthenocarpy occurs. Commercial-quality fruit can be produced in cool environments or in greenhouse winter production locations where pollination is limiting. Under summer growth conditions, normal pollination, fruit production, and seed set occurs. Hormone treatments cannot be reliably used under these conditions to induce parthenocarpy or increase fruit size. Seedless summer squash, zucchini, has been obtained by crossing two varieties, DG4 and Striata. This parthenocarpic variety is stable and has been used to produce additional commercial squash hybrids.

facultative capable of but not obligated to

Genetic engineering has been used to produce facultative parthenocarpic eggplants. A two-part gene transferred into eggplants consists of DefH9 from snapdragon (*Antirrhinum majus*) and iaaM from a fungus (*Pseudomonas syringae*). The iaaM gene produces the plant hormone auxin, while the DefH9 component restricts expression of the hormone gene to the immature fruit of the eggplants. Thus, the eggplants apply their own hormone treatment at the appropriate time and place. Conventional application of auxin on the surface of the fruit is ineffective in this case. Normal eggplant fruit are produced even when pollination does not occur, such as in winter greenhouse production. Fruit set and seed set are normal under favorable pollination conditions. In the future, this method could also be used for producing seedless fruits of many different species. SEE ALSO BREEDING; FRUITS; HORMONES; POLYPLOIDY; PROPAGATION; REPRODUCTION, SEXUAL.

Dwight T. Tomes

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Stinkhorn, *Dictyophora indusiata,* whose greenish-gray fetid-smelling spore mass and skirtlike indusium are both attractants for insects.

Fungi

Mycology is the study of fungi (*mykes*, Greek for "fungi," and *ology*, meaning "study of"). Most contemporary mycologists consider the fungi to be in two kingdoms: kingdom Fungi with five phyla and kingdom Stramenopila with three phyla. The total number of fungi in the world is estimated to be over 1.5 million with less than 5 percent of the species described. Some mycologists believe that the total number of fungi may be more than 2 million. Two other kingdoms are sometimes mistaken for fungi: the slime molds (kingdom Myxomycota), which have a creeping plasmodium, and the bacteria and **actinomycetes** (kingdom Monera).

Structure and Life Cycle

Fungi are nonphotosynthetic, lacking the chlorophyll of higher plants and algae, and are recognized by their fruiting bodies, which is the visible part of the fungus. Examples include mushrooms, puffballs, molds, cup fungi, and morels. The vegetative structure consists of minute **filamentous** cells called hyphae, which are microscopic in size, usually from 1 micron to 10 microns in diameter. An aggregate of hyphae is called a mycelium, which is the **thallus** or vegetative part of the fungus plant known as spawn in the mushroom industry. In the kingdom Fungi, the mycelium has one haploid nucleus per cell (only one set of chromosomes) or is dikaryotic (two **haploid** nuclei per cell). In contrast, in the kingdom Stramenopila, mycelium has diploid nuclei (one nucleus with chromosomes from both parents). In both kingdoms, the mycelium has rigid cell walls usually composed of chitin (a complex carbon **compound**), although it is infrequently made up of cellulose in kingdom Fungi.

In both kingdoms, fungi obtain their nutrition by excreting **enzymes** into the host or any organic material, which is then broken down and absorbed into the hyphal cell to provide the nutrition necessary for growth. Fungi function in the **ecosystem** as saprophytes, or decomposers. They break down dead organic matter as parasites by attacking living hosts or host cells, and as mycorrhizae (*mycor*, meaning "fungi," and *rhizae*, meaning "root") by forming jointly beneficial unions with the roots of higher plants. Fungi and algae combine to form a plant called a lichen. Only fungi and bacteria decompose various kinds of organic matter and change complex organic structures, such as plant cell walls containing lignin or the chitinous exoskeletons of insects, into simple carbohydrates that can then be assimilated by a wide variety of organisms.

The hyphae grow until they form an extensive mycelium of fungal tissue. At this point a young fruiting body initial (or button) begins to form and develops into a mature fruiting body. In some phyla fruiting bodies are large and variously recognized as mushrooms, boletes, puffballs, conks, cup fungi, morels, false morels, truffles, and witches' butter, to mention only a few. However, many of the aquatic fungi, molds, and other fungi (such as the yeasts) form minute fruiting structures that can only be seen with the aid of a magnifying glass or a microscope.

The function of the fruiting body is to form a tissue in or on which the spore-bearing surface is formed. The spore-bearing surface covers the gills of a mushroom, is inside the tubes of the bolete, or forms a spore mass inside the puffball and truffle. The spore of the fungus serves the same purpose as the seed of the green plants, but the spore is composed of only one or several simple cells. The spore forms following meiosis in sexual cells lo-

actinomycetes common name for a group of Gram-positive bacteria that are filamentous and superficially similar to fungi

filamentous thin and long

thallus simple, flattened, nonleafy plant body

haploid having one set of chromosomes, versus having two (diploid)

compound a substance formed from two or more elements

enzyme a protein that controls a reaction in a cell

ecosystem an ecological community together with its environment

cated in the spore-bearing surface. In the mushrooms, boletes, cup fungi, and morels, for example, the nearly mature spores are forcibly discharged at maturity from the spore-bearing surface. If one blows over the surface of a cup fungus at maturity, a small cloud (the puffing or a discharge of the spores) can be seen. However, in other fungi such as the puffballs, stinkhorns, and truffles, no forcible discharge occurs. The powdery spore mass of the puffball is often discharged through a pore in the top that forms at maturity. The greenish-gray spore mass of the stinkhorn emits a strong odor, which attracts insects that eat, contact, and spread the spores. The truffle, which is found at the surface of or beneath the soil, gradually matures and produces strong smells that attract small rodents that dig up and eat the fruiting bodies and distribute the spores.

Molds, such as *Penicillium*, produce microscopic asexual fruiting bodies that in turn produce asexual spores called conidia on structures known as conidiophores. Some yeast cells bud and reproduce asexually. Other fungi, such as the bread mold *Rhizopus*, produce asexual fruiting structures known as sporangiophores that support sacs called sporangia in which asexual spores are produced. Aquatic fungi also produce a variety of asexual spores, some of which are **motile** (called **zoospores**). These spores swim to a potential host, retract their **flagella**, and enter the host producing an oval fruiting body with a feeding tube or minute root-like rhizoids. The zoospores of the kingdom Fungi have one whiplash flagellum, while in the kingdom Stramenopila the zoospores have two flagella, one whiplash and one tinsel type, that move rapidly to propel the zoospore. Spores, either sexual or asexual, motile or nonmotile, usually germinate to form thin cylindric hyphal cells that rapidly elongate and branch to form the mycelium of the new fungus plant.

Penicillium, showing a conidiophore with asexual conidiospores.

motile capable of movement

zoospore a swimming spore

flagella threadlike extension of the cell membrane, used for movement

Nutrition

The fungus cell must grow into the host plant or a bit of organic material in order to gain nutrition from it. This is achieved by discharging enzymes (called exoenzymes) from the cells. Complex carbohydrates and proteins are broken down by this process and then are absorbed by the hyphae. The nutrients can then be **translocated** from one cell to another. The growth of most fungi is indeterminate (that is, it never stops) because the fungus must continue to grow into new areas to seek new sources of food. The typical fairy ring represents a visible bright green grass ring where the active mycelium is, and it is along this ring that the mushrooms will fruit. Each year the diameter of the ring will increase while the mycelium dies out in the middle because the food base is exhausted.

translocate to move materials from one region to another

Mycorrhizae

Mycorrhizal fungi invade the healthy outer cells of the tiny rootlets of higher plants. Ectomycorrhizae surround the rootlet with a sheath of fungal cells, and special hyphae penetrate between the **cortical** cells of the rootlet and exchange nutrients with the higher plant, usually a tree or a shrub. Endomycorrhizae called VA (vesicular arbuscular) mycorrhizae form oval storage cells (vesicles) and minute branchlike processes (arbuscules) in the root cells of the host where nutrients are exchanged. Because fungi do not carry out photosynthesis and cannot make their own sugar, the mycorrhizal fungus obtains moisture and carbohydrates from its green plant host and, in return, provides the host with nitrogen, phosphorus, zinc, and other es-

cortical relating to the cortex of a plant

Amanita virosa, a deadly poisonous mushroom common in the United States.

sential compounds. It does this using the miles of tiny mycelium to successfully compete for phosphorus and nitrogen, which extends the root system of the green plant. Most of the woody plants such as the pine, oak, birch, and beech have ectomycorrhizae, and most herbaceous plants such as grass, corn, wheat, and rye have VA endomycorrhizae.

Food, Drugs, and Poisons

Fungi play a major role in the diet of humans. Yeasts (*Saccaromyces cerevisiae*) are used in the process of fermentation, in which they break down carbohydrates to liberate carbon dioxide and to produce alcohol. Gin is made when juniper berries are fermented, wine from grapes, beer from grains, bourbon from corn, and scotch from barley. Yeasts are also used in making Limburger cheese, yogurt, and Kombucha tea. Baker's yeast produces a high proportion of CO_2, which causes the dough to rise. Molds, generally species of *Penicillium*, are used to produce cheese such as blue, Roquefort, and Camembert.

The new age of antibiotics was ushered in with Sir Alexander Fleming's discovery of penicillin in 1929. It was first produced by the blue-green mold *Penicillium notatum*. Many other antibiotics are produced from Actinomycetes. On the other hand, aflatoxins produced by species of *Aspergillus* cause food spoilage and are carcinogenic. Mushrooms also produce **toxins** that only affect humans when they are eaten. Examples of these are the amatoxins and phallotoxins produced by a mushroom, *Amanita virosa*, that are often fatal to humans; muscarine and muscimol produced by the fly agaric, *Amanita muscaria*, are usually not fatal. **Hallucinogens** such as psilocybin and psilocin are produced by several species of mushrooms including *Psilocybe cubensis* and the protoplasmic poison monomethyhydrozine (MMH) by the false morel *Gyromitra esculenta*.

toxin a poisonous substance

hallucinogenic capable of inducing hallucinations

Fungal Diseases

Fungi that are parasitic on humans include the common **dermatophytes** on the skin, hair, and nails, causing such diseases as barber's itch and ath-

dermatophytes fungi that cause skin diseases lete's foot (*Microsporium canis*). More serious diseases, such as *Histoplasma capsulatum* or histoplasmosis found in warm temperate climates and coccidiomycosis (*Coccidioides immitis*) in arid areas, grow in bird dung and soil, producing a respiratory infection in humans that is occasionally fatal. North and South American blastomycosis, sporotrichosis, and other diseases caused by fungi attack tissues and organs within the body and are incapacitating or fatal to their victims.

Diseases that affect major economic plants have historically impacted people. The ergot (*Claviceps purpurea*), which infects the grains of rye, produces deadly brown specks in bread and led to deformity and the death of thousands of people in the Middle Ages. The European grape was saved from the grips of the downy mildew (*Plasmopara viticola)* in the 1800s by the discovery of Bordeaux Mixture (copper sulfate and lime); the discovery gave birth to plant pathology as a science. The European potato famine, caused by the potato blight fungus (*Phytophthora infestans*), in the years 1845 to 1847 forced more than a million Irish to flee from Ireland. In the United States, the chestnut blight (*Cryphonectria parasitica*) has reduced the tall and highly valued American chestnut from the eastern forests to a rare shrub, while the Dutch elm disease (*Ceratocystis ulmi*) threatens to eliminate the American elm. Scientists struggle continually to produce resistant strains of wheat that will not be parasitized by the wheat rust (*Phytophthora infestans*) and corn that will be resistant to the corn smut (*Ustilago maydis*). Mexicans and Hispanic Americans cook the infected ears in many ways and consider them to be a delicacy.

The shelves of every supermarket have the meadow mushroom (*Agaricus bisporus*) and specialty mushrooms like Shiitake (*Lentinus edodes*), oyster shell (*Pleurotus ostreatus*), and the Portabello (*Agaricus* sp.) for sale. In fact, the leading agricultural crop in Pennsylvania is mushrooms. SEE ALSO Chestnut Blight; Dutch Elm Disease; Interactions, Plant-Fungal; Lichen; Mycorrhizae; Pathogens; Plant Systematics; Potato Blight; Taxonomy; Taxonomy, History of.

Orson K. Miller Jr.

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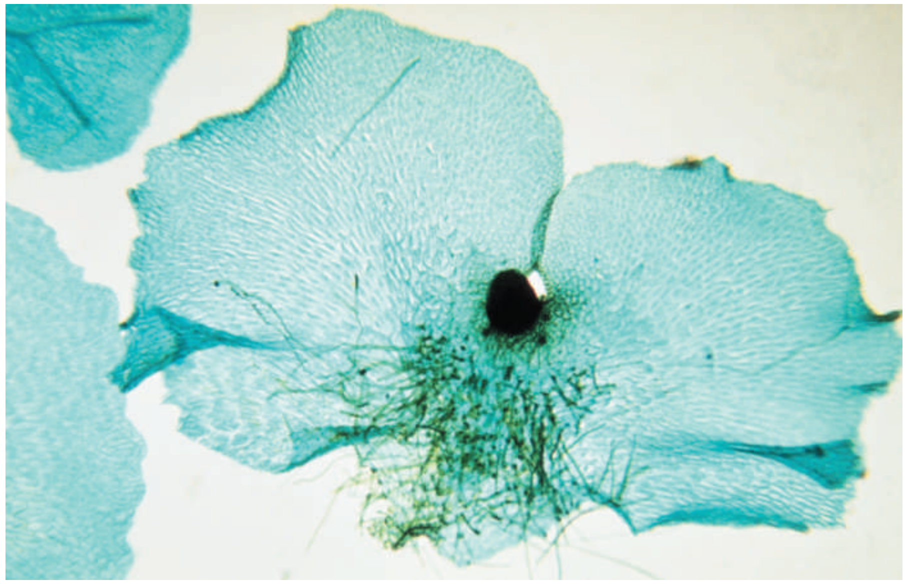
haploid having one set of chromosomes, versus having two (diploid)

sporophyte the diploid, spore-producing individual in the plant life cycle

Gametophyte

A gametophyte, or gamete-bearing plant, is one of the two multicellular phases that occur in alternation of generations. The gametophyte is the **haploid** phase; that is, its cells contain only one set of chromosomes, in contrast to the **sporophyte** phase, where the cells contain two sets. The gametophyte



Fern prothallia embryo and sporophyte.

develops from the germinating, haploid spore, which was produced by meiosis in the sporangium of the sporophyte phase. Gametophytes produce sperm and egg cells by **mitosis**, often in multicellular **gametangia** known as antheridia and archegonia, respectively. Fertilization, which occurs in the female gametophyte, establishes a new sporophyte generation. In some algae, like sea lettuce, the vegetative gametophyte is identical in form to the vegetative sporophyte, but in most organisms the gametophyte has a very different appearance from the sporophyte. In bryophytes the gametophyte is the highly visible, persistent phase of the plant, but in **vascular** plants the gametophyte is short-lived and often much reduced in size. Among land plants, gametophytes are of four different types. These include: (1) the green, leafy shoot systems of mosses, and leafy liverworts; (2) the green, **thallus** to prothallus forms of thalloid liverworts, hornworts, horsetails, most ferns, and some lycopods; (3) the colorless, subterranean, mycorrhizal axes of psilophytes and some lycopods; and (4) the small, **endosporic** forms of **heterosporous** lycopods, some ferns, and all seed plants. The smallest and least complex gametophytes are those of the flowering plants. The male gametophyte is the two- or three-celled pollen grain that is released from the anther, and the female gametophyte is the seven-celled embryo sac that is located in the base of the pistil of the flower. SEE ALSO Bryophytes; Reproduction, Alternation of Generations and; Reproduction, Fertilization and; Reproduction, Sexual; Sporophyte.

Barbara Crandall-Stotler

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

gametangia structure where gametes are formed

vascular related to transport of nutrients

thallus simple, flattened, nonleafy plant body

endosporic formation of a gametophyte inside the spore wall

heterosporous bearing spores of two types, large megaspores and small microspores

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Genetic Engineer

Plant genetic engineers create new varieties of plants, including row crops, vegetables and berries, forest and fruit trees, and ornamentals. These new varieties contain any number of new or improved traits, such as resistance

A lab technician monitors the growth of a sunflower plant raised from an embryo in controlled conditions as a genetic engineering project at the Sungene Technologies Laboratory in Palo Alto, California.

to pests and diseases, resistance to poor growing conditions, resistance to herbicides, and improved nutrition, wood quality, storage characteristics, and horticultural traits. Plant genetic engineers are also modifying plants to produce industrial **enzymes**, biodegradable plastics, pharmaceutical products, and edible vaccines. Plant genetic engineers collaborate closely with molecular biologists to identify and clone the necessary genes, and with plant breeders, who breed these into improved plant varieties.

enzyme a protein that controls a reaction in a cell

Genetic engineers are drawn to the discipline because of the power that creating new plant varieties has to help preserve crop yields, produce a better, healthier product for the consumer, and help safeguard the environment. Though some of the daily tasks can be routine and repetitive, the field is advancing rapidly, and mastering the new advances continuously provides challenges and prevents research and development from becoming routine.

Plant genetic engineers must have a strong background in biology, with an emphasis in botany, biochemistry, and genetics. An understanding of agriculture or forestry can be particularly helpful, especially for the selection of the traits to be modified. Plant genetic engineers begin with an undergraduate degree in one of the agricultural plant sciences, forestry, botany, genetics, biotechnology, or biochemistry, and many obtain an M.S. and/or a Ph.D. in these fields.

Those with B.S. and M.S. degrees usually work in a laboratory and handle the necessary deoxyribonucleic acid (DNA), plant cell cultures, and analytical work. Those with a Ph.D. set research goals and determine research directions. Salary range depends strongly on educational level. In 1999, people with a B.S. or M.S. may have earned \$20,000 to \$30,000 for an entry-level position, while entry positions for a Ph.D. degree were in the vicinity of \$50,000. Senior-level Ph.D. positions may have earned \$150,000. Chief areas of employment would be research universities, biotechnology companies, forest products companies, and international research centers. The greatest amount of genetic engineering takes place in the United States and Europe. However, because plant genetic engineering is taking place in many places of the world, there may be employment opportunities throughout the world.

toxin a poisonous substance

Very vocal groups of opponents to genetic engineering technology claim that genetic engineering will lead to genetic pollution, introduce **toxins** into the food supply, and damage the environment. Such opposition has led to bans on genetically engineered plants and food products in many countries, as well as an extensive patchwork of regulations. Sustained opposition to genetically engineered plants may limit employment opportunities in the future. SEE ALSO Breeder; Breeding; Genetic Engineering; Molecular Plant Genetics; Transgenic Plants.

Scott Merkle and Wayne Parrott

Genetic Engineering

Humans have been modifying the genetic constitution (genomes) of crop plants for thousands of years, since the very beginning of agriculture. In the past, modifying the genomes of crop plants was accomplished by selecting seeds from those individual plants that produced the most grain, were most resistant to diseases, or were most tolerant of environmental stresses (e.g., drought). These seeds were then used to plant the next year's crop. This approach is sometimes referred to as classical plant breeding, and it has been extraordinarily successful at producing improved crops. However, this approach is subject to a major limitation in that it only allows for the selection of genes (and the associated genetic traits) that are already present in the genome of the crop plant. Although many potentially useful genes are present in the genomes of other organisms, they are not always present in the genomes of crop plants.

The limitations of classical plant breeding can be partially addressed by facilitating sexual reproduction between a crop plant and a wild plant species. This approach can be used to introduce new genes into a crop plant genome (e.g., genes for disease resistance). Unfortunately, sexual reproduction between crop plants and other species is restricted to closely related plant species, limiting the pool of potential genes that could be added to the crop plant genome. For example, commercially grown tomatoes (*Ly-*

copersicon esculentum) may be able to reproduce sexually with wild tomato relatives (other members of the genus *Lycopersicon*), but they would not be able to reproduce sexually with any wild (or domestic) member of the grass family (species within the family Poaceae). In addition, no human-directed mechanism for introducing genes into plants from other types of organisms (e.g., bacteria, fungi, mammals, etc.) was available prior to the advent of genetic engineering.

Plant genetic engineering has been developed to circumvent the limitations of classical plant breeding, allowing the addition of genes (i.e., segments of deoxyribonucleic acid [DNA]) from any organism to the genomes of crop plants. Plants to which one or more genes have been added through a means other than sexual reproduction are called genetically modified organisms (GMOs) or transgenic plants. The genes that are introduced into the plants are referred to as transgenes.

The Process of Genetically Engineering Plants

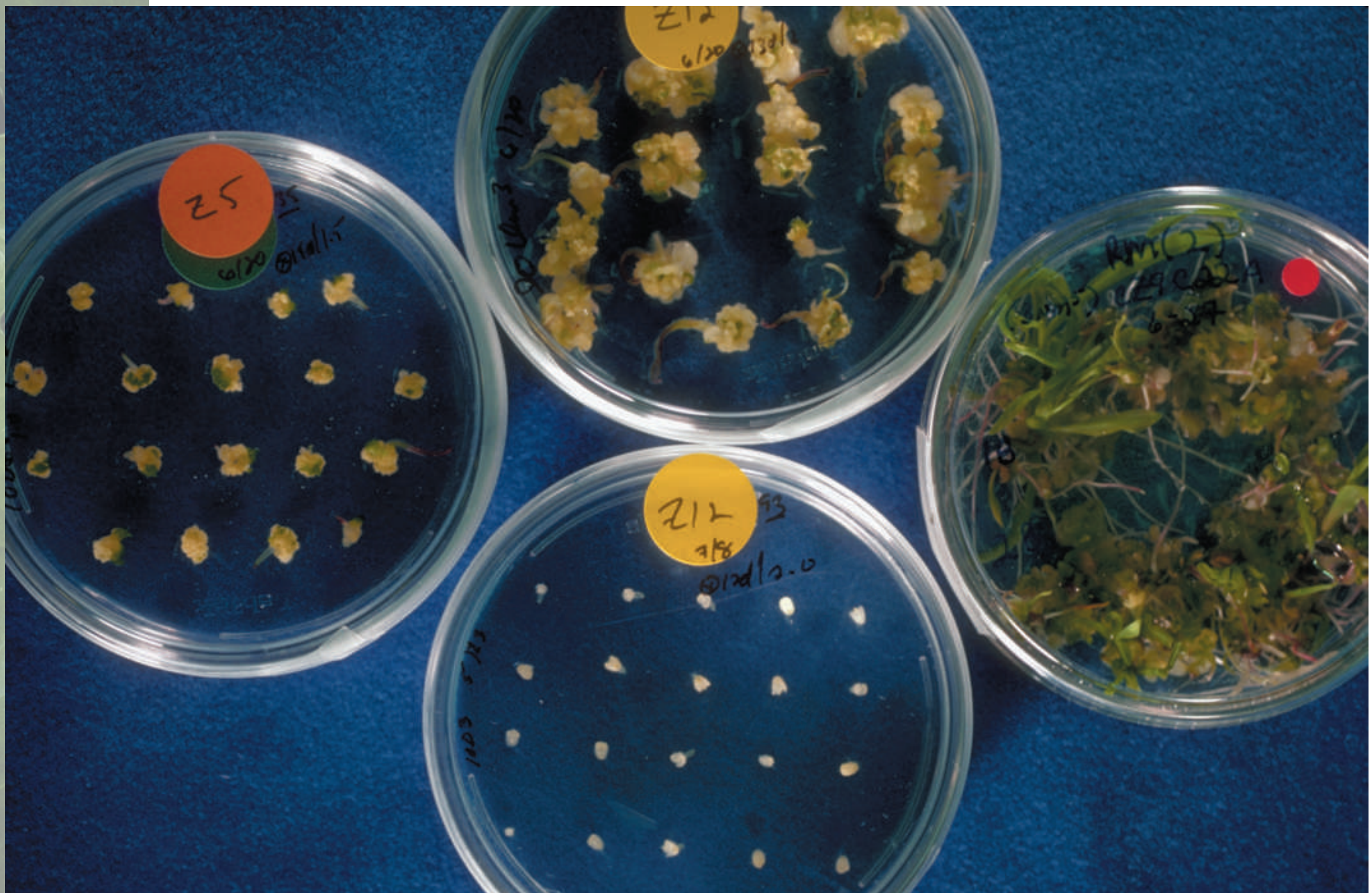
In order to achieve genetic engineering of plants, a series of tools and technologies are necessary. The ability to identify, isolate, and replicate specific genes is required. This series of steps is referred to as gene (or DNA) cloning. (A complete description of cloning is beyond the scope of this entry, but may be found in most biology textbooks.) A method to insert the cloned gene(s) into the genome of the crop plant is required, as is a method for identifying those cells that have incorporated the gene. The ability to regenerate entire plants from transgenic cells is essential, as is a means of verifying the presence of the transgene in the GMO.

Once a target gene has been cloned it is typically introduced into the genome of a crop plant by one of two means: *Agrobacterium*-mediated transformation or particle bombardment (biolistic) transformation. *Agrobacterium tumefaciens* is a very interesting soil bacterium that is a nonhuman "genetic engineer." Under natural circumstances, *Agrobacterium* has the ability to cause crown gall disease in some plants. The cause of the disease stems from *Agrobacterium*'s ability to insert some of its own genes into the genome of the plant. This results in the formation of a gall (tumorlike growth) on the plant and in the production of a food source, of which only the bacteria can make use. Deletion of the gall-inducing genes has allowed *Agrobacterium* to be used to produce many types of transgenic crop plants, including tomato, potato, and cotton.

Unfortunately, many important crop species are not easily susceptible to *Agrobacterium*-mediated transformation. The globally important cereal grains (such as corn, wheat, and rice) are prime examples of such species. Therefore, other approaches for introducing genes were developed. The most widely used is the particle bombardment technique. This technique involves accelerating small DNA-coated gold particles to a high velocity such that they are able to penetrate the cell walls of plant cells. Once inside the cell wall, some of the DNA is able to separate from the gold particles and integrate into the genome of the plant cell.

Regardless of whether the new DNA (transgene) is introduced by *Agrobacterium* or by particle bombardment, it is essential to understand that not all of the plant cells will contain the new gene(s). Therefore, a means of screening for the presence of the new DNA is required. Com-

A geneticist holds a test tube containing a cloned flowering plant.



Corn tissues at various stages of growth used by genetic engineers at the Sungene Technologies Laboratory in Palo Alto, California, to cultivate desired traits.

monly, this is accomplished by including additional genes in the introduced DNA whose protein products confer resistance to a **toxin** that would normally kill plant cells. For example, the phosphinothricin acetyltransferase (PAT) gene confers resistance to the herbicide Basta. If a population of plant cells is bombarded with DNA that includes the PAT gene, and subsequently the cells are grown on a medium containing Basta, only those cells that contain the newly introduced transgenes will be able to grow.

toxin a poisonous substance

The transgenetic cells must then be able to be regenerated into entire plants. This is accomplished through a series of steps referred to as tissue culture and makes use of plant hormones to stimulate the production of roots and stems from the transgenic cells. Various methods can be used to verify the continued presence of the transgene(s) in the regenerated plants. One method is to specifically amplify (thereby allowing easy detection) the DNA of the transgene using a technique called polymerase chain reaction (PCR).

An Example of a Genetically Engineered Crop Plant

To see how genetic engineering may be used to improve crops, let's look at a specific example. In the United States corn (maize) is attacked by an introduced insect pest called the european corn borer (ECB). This pest is a moth, and it is during the larval stage (the caterpillar stage) that it actually feeds on corn plants. Under some circumstances this pest can cause major damage to corn crops. There is also a naturally occurring species of bacterium (*Bacillus thuringiensis*) that possesses a gene encoding a protein toxin (Bt-toxin) that is quite effective in killing many species of caterpillars. In addition, the Bt-toxin protein is not toxic to mammals, birds, and most other animals. Clearly, this Bt-toxin gene cannot be introduced into corn via sexual reproduction, as corn plants and bacteria are unable to reproduce sexually. However, genetic engineering provides an alternate approach to introduce the Bt-toxin gene into the genome of the corn plant.

The Bt-toxin gene has been cloned from *Bacillus thuringiensis* and introduced into the genome of corn plants using the particle bombardment approach. The resulting transgenic corn plants are resistant to ECB, and are, in fact, capable of killing ECB larvae that feed upon them. In essence, these transgenic corn plants are producing their own internal insecticide, allowing the farmer to plant corn without needing to subsequently apply chemical insecticides to prevent damage caused by ECB.

Potential Benefits and Concerns Regarding the Widespread Use of Genetically Engineered Crops

What are the potential benefits of planting transgenic corn producing the Bt-toxin? Potentially, the yield of corn may increase as corn plants are protected from ECB. Depending on market conditions and the cost of buying the Bt-toxin producing corn seed, this may or may not represent an economic benefit for corn growers. However, if the corn crop had been routinely sprayed with chemical insecticides to control ECB (true in some parts of the corn belt), then that economic cost to the farmer would be eliminated. In addition, the environmental costs of spraying a chemical pesticide, which can result in extensive killing of nontarget species, would be minimized. There have been, however, various concerns raised about the widespread use of Bt-toxin-containing corn, so we should also consider the potential dangers of applying this technology.

The potential concerns with widespread usage of Bt-toxin containing corn fall into three primary categories: direct health impacts of Bt-toxin on humans, selection for Bt-toxin resistant populations of ECB, and unintended environmental impacts. Bt-toxin-containing insecticides have been used for many years, and there have been no indications of direct toxic effects on humans. Nonetheless, there is the possibility that some individuals could develop allergic reactions to this protein. Widespread human use of transgenic corn containing Bt-toxin could potentially expose a much larger number of people to this protein.

Development of Bt-toxin-resistant populations of ECB is also certainly a major area of concern. Such insects would be able to feed on Bt-transgenic corn and could potentially lead to increased populations of ECB. Other insects have demonstrated a remarkable ability to develop resistance to various insecticides (DDT-resistant mosquitoes, for example). Current approaches to minimize development of Bt-resistant ECB include planting mixtures of Bt-toxin containing corn and nontransgenic corn. The idea is to allow those corn borers that are susceptible to Bt-toxin to continue to reproduce, maintaining the presence of the susceptibility gene(s) in the ECB population. A related concern is that decreasing the population of ECB through widespread use of Bt-toxin-containing corn will result in a decline of the populations of other insects (principally types of wasps) that prey on ECB, reducing the potential for natural control of the ECB population.

The area of unintended environmental impacts is also of major concern. It is important to recognize that, while the Bt-toxin does not affect mammals or birds, it is toxic to many species of insects, not just ECB. Current commercially available Bt-toxin-containing corn varieties produce the toxin throughout the entire body of the plant, including the pollen grains. When a pollen grain is released from an anther it is dispersed by the wind in an attempt to reach the stigma (silk) of a female flower, but the vast majority of the pollen grains never reach a silk; they land somewhere else. If that somewhere else is a plant leaf that serves as a food source for another species of insect, that nontarget insect may be harmed or killed by the Bt-toxin. This concern has been specifically raised with regard to the monarch butterfly, whose caterpillars feed on milkweeds in and near corn fields; but there are, of course, many other species of moths or butterflies that could be potentially affected. Further studies are in progress to assess the impact of pollen-born Bt-toxin on monarch or other butterfly or moth species. One possibility to minimize this problem is to eliminate production of the Bt-toxin in the pollen grains, while continuing production in those plant parts most affected by ECB, principally the stems and ears. This approach will necessitate the development of new varieties of Bt-toxin-containing transgenic corn that include the appropriate gene-regulating elements.

Clearly, the use of genetic engineering to modify crop plants has the potential to greatly benefit humans. Increased crop productivity could be used to feed the still-increasing population of humans on our planet. Increased production might also allow preservation, or restoration, of some natural areas that would otherwise be required for agricultural purposes. Other plant genetic engineering strategies may allow production of crops with improved nutritional qualities, the ability to synthesize industrial feedstocks, resistance to various types of environmental stresses, or even the ability to produce drugs used in human medicine. However, as the Bt-toxin-containing corn example demonstrates, it is essential that we investigate, as thoroughly as possible, what unintended consequences may arise from use of the technology prior to widespread adoption of a particular type of transgenic crop plant. SEE ALSO Breeding; Genetic Engineer; Tissue Culture; Transgenic Plants.

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Genetic Mechanisms and Development

Development in plants refers to the formation of shape and pattern in the multicellular organism. While development can be influenced by environmental factors such as light or temperature, the major factor controlling development of any plant is, of course, its genes. Genes determine the overall shape and size of the mature plant, its branching pattern and leaf type, the extent and arrangement of **vascular** tissue in root and shoot, and the timing of flowering and the form of flowers produced.

vascular related to transport of nutrients

In plants the genetic mechanisms that control developmental events are best understood in the case of flower development. A normal (wild type) flower of most **angiosperms** (flowering plants) has four distinct types of organs that are arranged in four concentric rings (whorls). The outermost whorl has green, leaflike organs called **sepals**. The second whorl from outside consists of brightly colored organs called petals. The third whorl consists of stamens, which are male reproductive structures that make pollen. The innermost whorl consists of female reproductive structures called carpels. Although the number and shape of these organs differ from species to species, they are genetically determined and develop sequentially from outside to inside (sepals, petals, stamens, and carpels). All floral organs develop from a small group of undifferentiated cells known as the floral meristem.

angiosperm a flowering plant

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

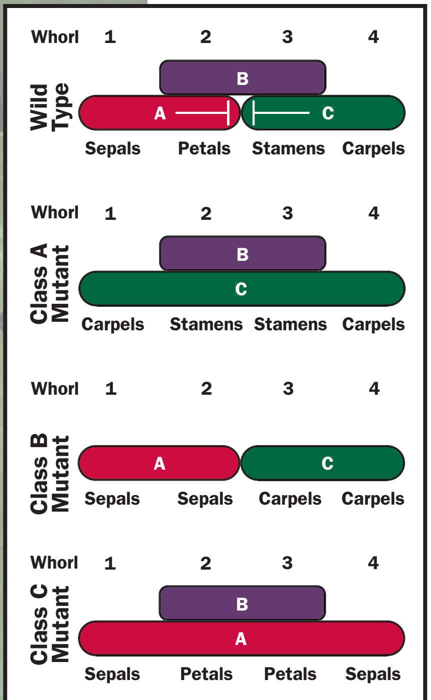
The genetic basis for this pattern formation was not known until recently. During the 1990s enormous progress was made in identifying the genes that determine the floral organ identity. Much of this information came from genetic studies with *Arabidopsis thaliana* (mouse ear cress or thale cress), which belongs to the mustard family, and *Antirrhinum majus* (snapdragon). A normal flower of *Arabidopsis* has four sepals, four petals, six stamens, and two carpels. Genetic studies with *Arabidopsis* and snapdragon indicate that three classes of genes (called class A, B, and C) work together to determine the organ identity and are responsible for the development of the right floral organs in the right place.

In *Arabidopsis,* A-class genes include two genes (*APETALA1, AP1; APETALA2, AP2*); B-class has two genes (*APETALA3, AP3; PISTILLATA, PI*); and C-class has one gene (*AGAMOUS, AG*).

Each class of genes acts in two adjacent whorls in a combinatorial fashion to specify organ identity. Whether the cells in the floral **meristem** develop into a particular organ will depend on the expression of one or two of these classes of genes. Class A genes are active in whorls 1 and 2, Class B genes function in whorls 2 and 3, and class C genes are active in whorls 3 and 4. The activity of class A genes alone leads to the development of sepals, expression of A and B in cells leads to petal development, B and C class genes are necessary for stamen development, and the activity of C class alone allows carpel development. In addition, A activity inhibits the expression of C class and vice versa such that C activity is found in all four whorls of A mutants whereas A activity is found in all four whorls in C mutants.

meristem the growing tip of a plant

This model has been supported by several kinds of genetic tests by creating single, double, or triple mutations in ABC genes, expression analysis of these genes, and also by artificially expressing A, B, and/or C genes in wrong whorls. Because A inhibits C, inactivation of A results in expansion of C activity into the first and second whorls, and to the development of carpel-like structures in place of sepals (C acting alone) and stamens in place



The "ABC" model, which explains the specification of floral organ identity by three classes of genes. Numbers on the top indicate four whorls in the flower. The activity of the A, B and C class genes in each whorl of the wild type is indicated in the top panel. The sign ⊢ indicates the inhibition of A activity by C and vice versa. Mutants affecting the A (class A mutant), B (class B mutant), or C (class C mutant) function result in changes in organ identity as shown in the figure.

of petals (C acting with B). Where B is inactivated, stamens are converted to carpels and petals to sepals. When C is inactivated, the presence of A activity in the third and fourth whorls leads to conversion of stamens to petals and carpels to sepals. In plants lacking both B and C genes, class-A genes are expressed in all four whorls, leading to a flower with sepals in all four whorls. Overexpression of class-B genes in all four whorls results in a flower consisting of petals in the first and second whorls and stamens in third and fourth whorls. Inactivation of all three classes of genes results in a flower that has leaves in all four whorls, indicating that the floral organs are modified leaves consistent with theories of floral evolution.

Although the mechanisms through which the activity of ABC genes specifies the floral organ identity are not clear, it is likely that they regulate the expression of other genes that are involved in the development of a specific floral organ. This speculation is supported by the fact that four of the five genes that belong to ABC classes encode **transcription factors**. How these organ identity genes are turned on at the right time and in the right cells of the floral meristem is not completely understood. SEE ALSO Differentiation and Development; Embryogenesis; Flowers; Germination and Growth; Hormonal Control and Development; Hormones; Molecular Plant Genetics; Senescence.

A. S. N. Reddy

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Germination

Seeds are usually shed from their parent plant in a mature dry state. The dry seed contains an embryo that is the next generation of the plant in miniature. Before the seed can grow, however, it must first emerge from the seed and establish itself as an independent, photosynthetic seedling. Germination, by definition, starts when the seed takes up water, a process known as imbibition, and is completed when the embryonic root, the radicle, penetrates the outer structures of the seed (usually the seed coat and, in some species, the surrounding storage tissues of the **endosperm**).

In the mature dry state, the seed is metabolically inactive (quiescent) and can withstand environmental extremes of temperature and drought. When water enters the seed during imbibition there is a leakage of **solutes** (ions, sugars, and amino acids) because cell membranes are temporarily unstable during hydration. Cellular metabolism recommences within minutes after imbibition begins, using cell components and **enzymes** that were present in the dry seed. Respiration to provide energy and protein synthesis to produce new enzymes that support metabolism are important early events in germination.

transcription factors proteins that bind to a specific DNA sequence called the promoter to regulate the expression of a nearby gene.

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

solute a substance dissolved in a solution

enzyme a protein that controls a reaction in a cell

A germinating corn kernel.

Following imbibition, there is a period when no further water is taken up (plateau phase) and during which metabolism proceeds to ready the seed to complete germination. Restitution of cellular damage resulting from drying and imbibition is completed (e.g., DNA and mitochondria are repaired), and new enzymes and other proteins are synthesized. Elongation of the cells of the radicle is responsible for its emergence from the seed. Their cell walls become more stretchable and the internal water pressure (turgor) of the cells causes them to expand. Cell division and deoxyribonucleic acid (DNA) synthesis occur after radicle emergence, and later the mobilization of food reserves occurs within the storage organs of the seed to provide nutrients for post-germinative growth.

In some seeds the embryo is surrounded by a storage tissue that is sufficiently rigid to prevent extension of the radicle and completion of germination. This tissue frequently has thickened hemicellulose-containing cell walls, and a reduction in their resistance is necessary to permit radicle penetration. This might be achieved by cell-wall hydrolases or cell-separating enzymes, perhaps induced in the storage tissue in response to hormones released from the embryo late during germination.

Seeds of many noncultivated species, such as weeds, are often **dormant** when mature. When imbibed, these seeds exhibit the same intense metabolic activity as non-dormant seeds but do not complete germination. Germination does not occur unless the seeds receive an external **stimulus** (e.g., low or fluctuating temperatures, or light) while in the imbibed state. The

dormant inactive, not growing

stimulus trigger

plant hormone abscisic acid plays some role in inducing dormancy during seed development, and its application to many seeds can prevent radicle emergence. Conversely, the plant hormone gibberellic acid, when applied in low concentrations to dormant seeds, will promote the completion of germination. How abscisic acid and gibberellic acid control germination is not known. SEE ALSO GERMINATION AND GROWTH; HORMONES; SEEDS.

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Germination and Growth

A seed is an enclosed, protected package of cells surrounding a miniature plant, the embryo, that can grow to form a copy of the plant bearing it. Seeds thus serve to spread and **propagate** plants, but they can also help the plant survive unfavorable climatic conditions, such as a freezing winter, in the form of the protected embryo.

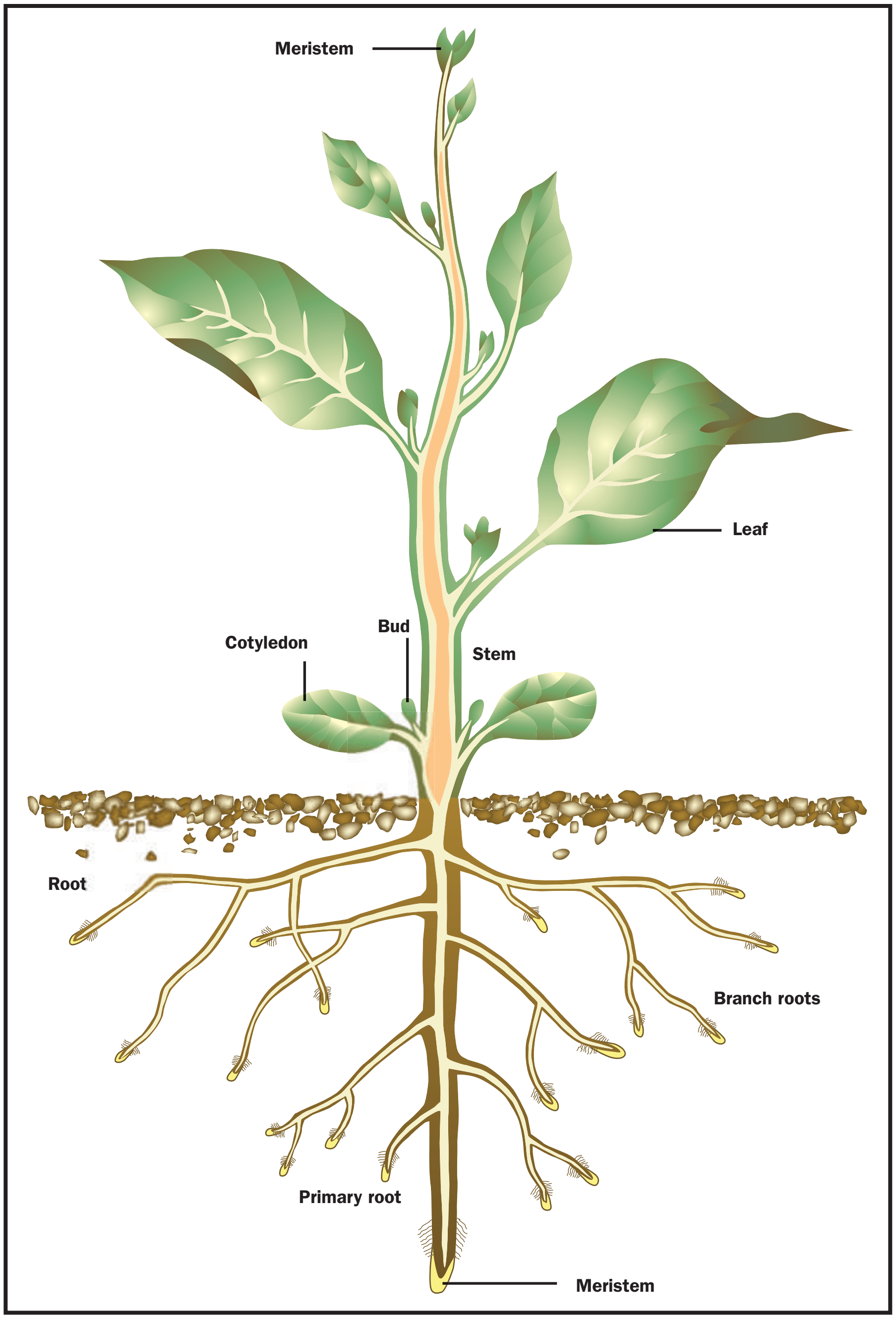
propagate to create more of through sexual or asexual reproduction

A typical seed consists of three main parts. The outer layer, or seed coat, protects the interior contents against drying out, infection, attack by predators, and noxious chemicals in the environment; it may also bear hooks or other structures that attach the seed to passing animals, aiding dissemination. The innermost structure is the embryo, complete with root tip, stem tip, and specialized seed leaves called cotyledons. Between these two structures lies the endosperm, cells containing stored food that the embryo digests and uses as an energy source when it starts to grow. Sometimes, as in beans, the stored food is in the cotyledons of the embryo rather than in separate endosperm cells.

Seeds are drier than growing plant cells, and as a result are **dormant**. Germination begins when the seed absorbs water and the cells of the embryo elongate, pushing the root tip beyond the seed coat. To accomplish this, the embryo mobilizes the food reserves of the endosperm by secreting the hormone gibberellin, which travels to the endosperm. When gibberellin reaches its target cells in the endosperm, it stimulates gene activity, causing the production of digestive enzymes that break down stored starch, proteins, and fats into simpler molecules that can be burned (oxidized), thus furnishing energy for growth.

dormant inactive, not growing

Seeds are formed from ovules located in the ovary in the center of the flower. These highly hydrated cells become partially dehydrated and dormant in response to accumulation of another hormone, abscisic acid (ABA), produced by the mother plant and transported into the seed. Before becoming active and germinating, the seed must first destroy part of its ABA content. Without ABA to confer dormancy, the seed might germinate prematurely on the mother plant, negating its function of dissemination. Without the water-removing action of ABA, seeds could not withstand freezing temperatures and other unfavorable climatic conditions.



Areas of plant growth. Redrawn from Galston, 1994, p. 11.

Some seeds can lie dormant for years before germinating. A Chinese lotus seed is known to have germinated after at least three centuries of dormancy, and even longer dormancies have been claimed. Such deep dormancy requires an especially rugged and nonporous seed coat, made of hard, strong materials, and covered by water-resisting waxes, resins, and lacquerlike materials. Before such seeds can germinate, the coats must be made permeable, either by mechanical force or by chemical or microbial action. Some dormant seeds germinate when treated with gibberellin or another plant hormone, cytokinin; these hormones work against the effects of ABA. Certain seeds are sensitive to light, requiring some illumination before becoming active. This is due to activation of a pigment called phytochrome, which

Broad bean *Vicia faba* germinates when suspended over water or in a medium of sodden paper.

also regulates seedling growth and development. The light requirement ensures that the seed will not germinate if it is buried too deeply in the soil to be able to reach the surface before its stored food supply runs out.

Germination occurs when the root protrudes from the seed coat. Root emergence is followed shortly by the emergence of the stem from the other end of the seed. The root grows downward, towards the center of gravity of Earth, while the stem grows upward. It is not yet understood why these organs behave oppositely toward gravity, but it appears that in both, gravity is sensed by the falling of heavy particles in the cells. Their opposite behavior toward gravity makes it likely that roots will find their way to water and minerals in the soil, while leaves will find the light needed for food synthesis. The orientation of plant organs is also affected by light, which generally causes stems to turn towards the light, roots away from the light, and leaf blades to become perpendicular to the source of light.

Growth and Development

meristem the growing tip of a plant

The embryo has a bipolar axis, with a region of cell division retained at each end. These regions, called **meristems**, maintain this activity throughout the life of the plant. The meristem at the stem apex includes an outer layer, whose cells divide in only one plane to produce more surface area, and an inner layer whose cells divide in all directions to produce the interior bulk. From these layers are produced more stem, leaves, and ultimately flowers. By contrast, the root meristem produces only root tissue, covered at its apex by a root cap, whose hardy cells protect the delicate internal meristem region as the root pushes into the soil.

Whenever leaves are formed, **lateral** buds are also formed in the angle between leaf base and its insertion into the stem.

lateral away from the center

Each lateral bud contains a meristem, which is generally kept inactive by the downward diffusion of the hormone **auxin**, which is produced by the dominant bud at the apex. If this apical bud is injured or removed, or if there is an unusually large supply of cytokinin from the roots, a lateral bud may become active or even dominant.

auxin a plant hormone

When a seed germinates in darkness, the seedling stem is long, slender, and unpigmented, and may terminate in an apical hook that protects the delicate meristem during upward growth through the soil. The hook is formed in response to the gaseous hormone ethylene. When the seedling is illuminated, activation of phytochrome turns off ethylene production, opens the hook, inhibits further stem elongation, promotes leaf blade expansion, and initiates the synthesis of chlorophyll. In both stem and root, the area just behind the tip elongates the most, as a result of the elongation of young preexisting cells. SEE ALSO Differentiation and Development; Embryogenesis; Germination; Hormones; Hormonal Control and Development; Meristems; Phytochrome; Seed Dispersal; Seeds; Tropisms and Nastic Movements.

Arthur W. Galston

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Gibberelins

See Hormones.

Ginkgo

Ginkgo biloba is a woody tree with a spreading form and a large trunk that reaches a height between fifty to eighty feet. The trees are sexually dimorphic (two-forms), and male trees typically have steep branching angles while female trees are broadly branched. Ginkgo grows in temperate climates and is long-lived, with trees up to one thousand years old having been reported.

Ginkgo is characterized by flattened, often bilobed leaves, with numerous fine veins that lack a midvein. Leaves are clustered on slow-growing, short shoots or spaced spirally on elongated shoots. Ginkgo trees are deciduous and the silhouettes of its bare branches make it easy to identify male and female trees. The pollen of Ginkgo is called prepollen because it pro-

The leaves of a *Ginkgo biloba* tree.

haustorial related to a haustorium, or food-absorbing organ

duces a **haustorial** tube upon germination and only after several months releases a motile sperm cell that swims to fertilize the egg. Ginkgo is one of the most advanced land plants still fertilized by motile sperm cells. Ginkgo is a gymnosperm that produces specially modified plumlike seeds that, even though they look like fruits, botanically are seeds. The seed is surrounded by a thin papery inner seed coat, a middle shell-like hard seed coat, and a fleshy outer seed coat that ripens to a soft, pulpy, foul-smelling mass when the seeds are dropped from the female trees.

lineage ancestry; the line of evolutionary descent of an organism

Tertiary period geologic period from sixty-five to five million years ago

Ginkgo biloba has a long history, with ancestors extending back some 280 million years into the Permian. It is one of very few plants living today that has such a clear lineage dating back into the Paleozoic era. During the Mesozoic era the Ginkgo **lineage** diversified and spread to many parts of the world. During the Cretaceous, there were seven to ten species of Ginkgo trees living, and they would have been a common sight among the dinosaurs of the Northern Hemisphere. Fossil Ginkgo leaves and petrified trunks can be found during the **Tertiary period** in North America, Europe, and Asia where trees lived until less than five million years ago.

propagate to create more of through sexual or asexual reproduction

There is now only one living species in the family Ginkgoaceae, a once diverse and widespread group, and it is indigenous to only a small area in China. Although nearly extinct in the wild, it has been preserved as a living fossil because it was planted at the entrances to Chinese and Japanese temples. Ginkgo has commonly been planted as a street tree in temperate North American cities (such as Washington, D.C.). Male trees are often vegetatively **propagated** for this purpose because they lack the foul-smelling, fleshy fruitlike seeds. Ginkgo trees are quite tolerant of city pollution.

flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

The cleaned seeds and leaves are reported to have beneficial health effects on the brain, hearing, eyes, lungs, kidneys, liver, and general circulation. The seeds are eaten and the leaves used to prepare tea. It is used for its antibacterial effects and benefits for nerves, asthma, vision, improving blood flow, and slowing aging. Several secondary metabolites such as **flavonoids**, terpenoids (e.g., ginkgolides A, B, and C, bilobalide, ginkgetin, and isoginkgetin), and organic acids are some of the chemicals isolated from

Ginkgo. Extracts of Ginkgo are sold as a health diet supplement. SEE ALSO Evolution of Plants; Gymnosperms; Systematics, Plant; Taxonomy; Trees.

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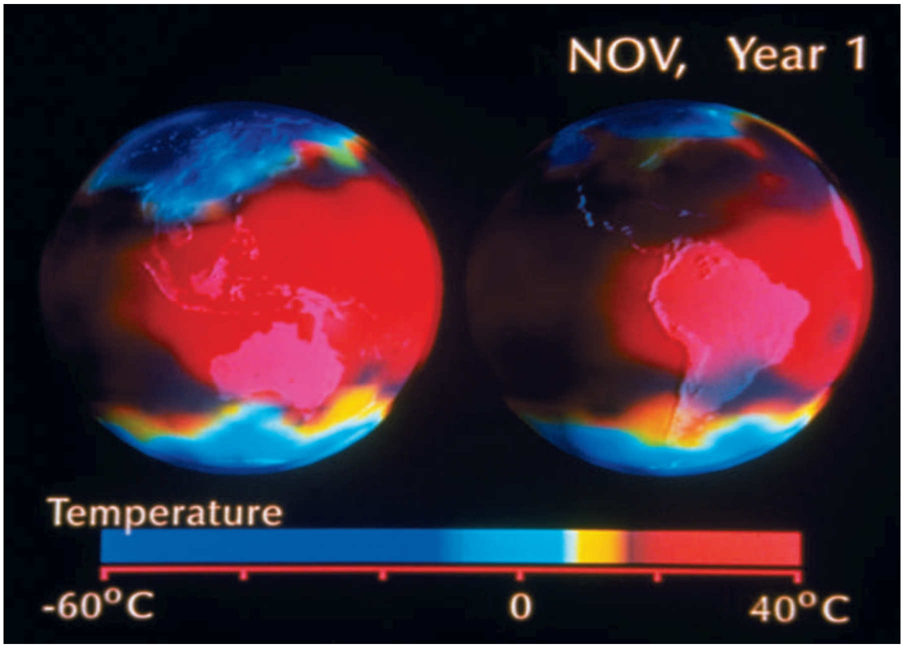
Global Warming

The term *global warming* simply means that the global climate is warming. Humans are popularly assumed to be the cause of global warming. Further, global warming is usually assumed to be harmful to humans and to plant and animal life. Global warming is a commonly discussed and debated scientific topic both in the media and in the scientific community.

Scientific Debate: Existence, Extent, Causes, and Pace

Nearly all of the scientific community agrees that based on surface temperature observations, the global climate warmed by about 0.5° C in the twentieth century. Satellite observations of global temperatures show warming trends between 1970 and 1990 similar to those found in surface observations. Decreases in sea ice cover and global glacier retreat provide corroborating evidence of global warming. A few scientists believe that the warming at weather stations is due to the development of cities around weather stations, but analysis in the late 1990s has shown that warming is similar at urban and rural areas. Different areas of the world and different seasons have warmed more than others. Due to global atmospheric circulation patterns that transport heat from the tropics to the poles, warming has been greatest in high latitudes. In some areas of Alaska and Asia, average temperatures have warmed by over 4°C. Warming has also been greatest in spring months, particularly March, and in nighttime minimum temperatures much more than in daytime maximum temperatures.

While the presence of global warming is not seriously debated, its causes are. Greenhouse gases, including carbon dioxide, trap heat radiated from Earth and reemit some of it back to the ground. Without greenhouse gases, our planet would be uninhabitably cold. As shown by research on air bubbles trapped in ice cores, high temperatures have been associated with high levels of greenhouse gases during the geologic past. Most human-made carbon dioxide is produced by cars and industrial activity. As a result of fossil fuel burning, carbon dioxide levels have increased from 280 parts per million in preindustrial times to more than 360 parts per million by the late 1990s. Scientists believe that the pace of greenhouse gas emissions in the late twentieth century is partially responsible for the recorded temperature increases. This is called the enhanced greenhouse effect. A minority of scientists believe that natural processes, such as increased sun spot activity, account for the observed warming. However, statistical analysis shows that compared with the enhanced greenhouse effect, these other processes are highly unlikely causes of the observed warming.



Year 1 of a simulated greenhouse effect. The temperature is coldest at the poles and graduates to the highest temperature around the equator.

negative feedback a process in which an increase in some variable causes a response that leads to a decrease in that variable

positive feedback a process in which an increase in some variable causes a response that leads to a further increase in that variable

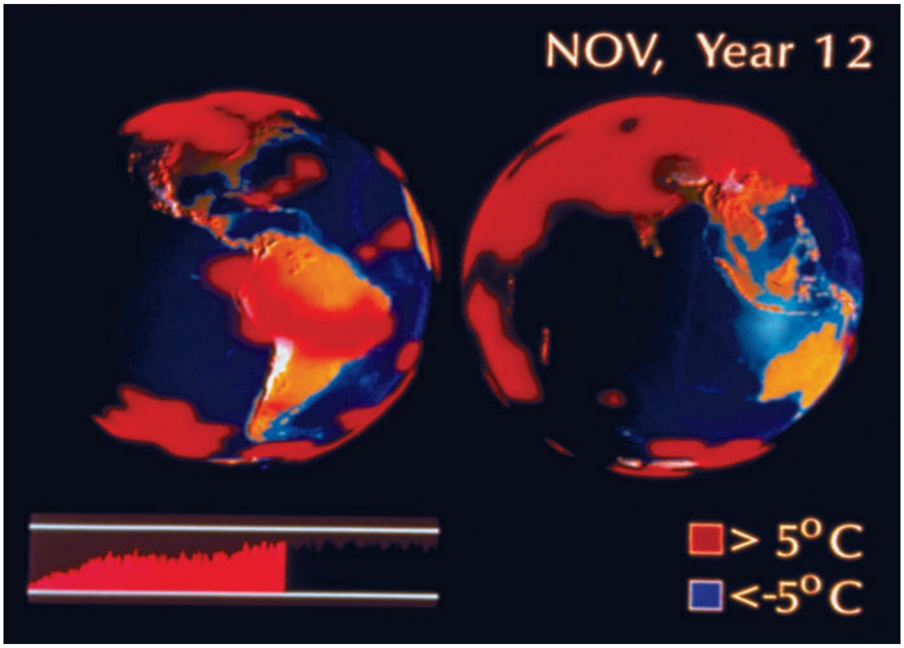
Computer models called global circulation models (GCMs) predict that warming will continue to increase. Due to processes called **negative feedbacks** that reduce global warming, there is some uncertainty over how rapidly warming will occur. Clouds, for example, are a result of evaporation. In a warmer climate, more evaporation will occur, leading to more clouds. Most types of clouds reflect solar radiation; this would act to cool temperatures. Other processes can act as **positive feedbacks** that increase global warming. Sulfur particles emitted from factories block radiation and thus cool temperatures. In an ironic twist, making factories cleaner could actually increase global warming. Accurately considering the complex network of feedbacks is a critical field of global warming research. In spite of these uncertainties, GCMs consistently predict further global warming.

The pace at which record high temperatures are being broken is increasing. The years 1998, 1997, 1995, and 1990 were the warmest since at least 1400 C.E. The twentieth century was also the warmest century since at least 1000 C.E. The bulk of observational evidence shows that not only is warming occurring, but that it is occurring at a progressively more rapid pace. Scientists researching past climates have shown that during glacial and interglacial periods, global temperatures (and carbon dioxide levels) have changed by more than the 0.5 degree (and 25 percent) currently seen. If plants and animals have survived these past changes, why should we be concerned about present changes? The answer is that the rate of greenhouse gas and temperature increase appears to be unprecedented. There is no guarantee that **ecosystems** and the people that depend on them will be able to adjust to the predicted levels of global warming.

ecosystem an ecological community together with its environment

Plant-Atmosphere Interactions

Global warming effects on plants depend on the existing climate and vegetation, but in general, there are three main categories of potential effects. First, for plants existing in climatic extremes, global warming may have



Year 12 of a simulated greenhouse effect. Note the irregularly shaped warm areas over Asia, North America, and Antarctica.

drastic impacts. For example, plants requiring cold temperatures may be forced off of mountain peak habitats. If this is their only habitat, extinction will occur. Second, global warming is likely to cause large shifts in biome distribution. Coniferous forests will shift farther north and grasslands and deserts will expand. Third, global warming can alter how plants function in their existing environment. For many areas, global warming is likely to lengthen the growing season, causing an increase in photosynthesis. Multiple observations show that the growing season has already significantly lengthened, especially in northern latitudes. For most plants, alteration in plant function without causing their extinction or displacement is the most likely consequence of global warming.

While people usually think about the effects of global warming on plants, plants can also moderate the effects of global warming. Only about half of the carbon dioxide put in the atmosphere remains there; the other half is taken up by Earth. Some of it is dissolved in the ocean, but plants take up some of it too. Plants are therefore acting to slow the pace of the enhanced greenhouse effect. Plants and especially trees are storing some of the carbon dioxide in wood. Unfortunately, this process is unlikely to continue forever. Eventually, when trees and shrubs die, the carbon stored in wood will enter the soil and will begin to decompose. Increased temperatures will cause high rates of decomposition, leading to an accelerated release of carbon dioxide from the soil. Consequently, it is likely that at a global level, ecosystems will begin to release carbon dioxide. Only by reducing fossil fuel emissions, a very difficult task both politically and economically, will we reduce greenhouse gasses. SEE ALSO ATMOSPHERE AND PLANTS; CARBON CYCLE; HUMAN IMPACTS.

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Grains

Grain crops of the world include the food grains, the coarse or feed grains, and a few minor coarse grains. The food grains include rice (*Oryza sativa*) and wheat (*Triticum aestivum*); the coarse or feed grains are barley (*Hordeum vulgare*), maize (*Zea mays*), rye (*Secale cereale*), oats (*Avena sativa*), millets (*Pennisetum* and *Setaria* species), sorghum (*Sorghum vulgare*), buckwheat (*Fagopyrum esculentum*), and triticale X (*Triticosecale wittmack*). Except for buckwheat, virtually all of the grain crops are members of the grass family. The principal harvestable commodity of these crops is the grain. Grazing or hay production is a minor use of a few crops.

All of the grain crops now are distributed worldwide, although each crop generally originated in a specific region: rice in Asia; wheat, barley, oats, and rye in the Fertile Crescent of the Mideast; maize in Central America; sorghum and the *Pennisetum* millets in Africa. Triticale is a human-made grain produced within the twentieth century by hybridizing wheat and rye.

Total production of the two major food grains in 1999 was very similar: 589 Mmt (million metric tons) of rice from 153 Mha (million hectares) and 584 Mmt of wheat from 214 Mha. Much more rice is irrigated than wheat, which results in higher yields and accounts for the

Three different grains used in the manufacture of whiskey.

essentially equivalent production of rice from fewer hectares than wheat. Coarse grain production in 1999 was 900 Mmt, from 314 Mha. Maize, with 604 Mmt from 139 Mha, was by far the most prominent coarse grain.

Rice is typically consumed as whole grain boiled white rice, while wheat is ground into flour for bread making. Coarse grains are generally fed directly to animals as whole or cracked grains, but small amounts of these crops also are used for food, usually as a ground product or in porridges, especially in the respective regions of origin, for example, maize in Central America, and sorghum and millets in Africa. Barley is used worldwide in brewing, while oats, maize, and wheat are used in many processed cereals. Rye is still used in bread making in Europe and the United States, but food use consumption of this crop declined dramatically fifty years ago when it was recognized that the fungal disease ergot that infects rye grains caused the mysterious malady known as St. Anthony's fire, which can result in convulsions and death.

All of the grain crops are cultivated as annuals: rice, maize, sorghum, and *Pennisetum* millets as summer crops; while wheat, barley, oats, rye, and *Setaria* millets are cultivated both as winter crops and as spring crops. The winter versions are grown in mild climates while the spring versions are predominant in the northern regions, such as the former Soviet Union, the northern Great Plains of the United States, and northern China. Winter versions generally yield more than spring versions, because the growing season is much longer for the former.

The Green Revolution refers to the shortening of the stems of rice and wheat, which began in the 1960s and which has often led to doubling of yields. Shorter stemmed versions of the other grain crops have also been produced, especially in sorghum. SEE ALSO AGRICULTURE, MODERN; AGRONOMIST; BORLAUG, NORMAN; CORN; ECONOMIC IMPORTANCE OF PLANTS; GRASSES; GREEN REVOLUTION; RICE; SEEDS; WHEAT.

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Gramineae *See Grasses.*

Grasses

The grass family, known scientifically as either the Poaceae or Gramineae, is one of the four largest families of flowering plants, with approximately five hundred genera and ten thousand species. Grasses range from tiny inconspicuous herbs less than 5 centimeters tall to the giant bamboos, which grow to 40 meters tall. The family is undoubtedly the most important flowering plant family to humans, directly or indirectly providing more than three-quarters of our food. In addition, grasses are major producers of oxygen and a large component of environmental filtering processes due to the enormous geographic range, spatial coverage, and **biomass** of grasses on Earth. Grasses are the greatest single source of wealth in the world.

biomass the total dry weight of an organism or group of organisms

Grasses are the greatest single source of wealth in the world.

Morphology

All grasses have fibrous secondary roots (the primary root disappears early in development) and can be annual or perennial, in which case they usually have underground stems called rhizomes. These can be very short and knotty or very long. In some species the rhizomes can go for several meters. Sometimes these stems run horizontally above ground and are then called stolons. Grasses characteristically have stems that are round and usually hollow with a node (the swollen areas along the stem where the leaves and branches are attached) and internode (the part of the stem between the nodes) arrangement. Their leaves are attached at the nodes and consist of two parts. The sheath clasps the stem (also known as the culm) sometimes all the way up to or beyond the next node. The blade is the upper part of the leaf that is free from the stem. The fact that the top edges of the sheath may overlap each other around the stem but are not joined to each other is a defining characteristic of grasses. At the point where the blade joins the sheath, there may be a flap of tissue called a ligule. This structure keeps dirt and parasites from getting into the space between the sheath and the stem.

The tiny grass flower, called a spikelet, is actually a composite of one or more tiny flowers and is the most characteristic structure among grasses. It is generally composed of two bracts called glumes, with one to many tiny flowers called florets attached above them. Each floret consists of a bract called a lemma that generally wraps around a smaller and generally very thin bract called a palea. These two encase the nearly microscopic rudimentary petals called lodicules, the stamens (usually one to three), and the ovary, which can have two or three feathery stigmas at its apex. There may be only a few spikelets on a plant but usually there are many (sometimes hundreds) arranged variously in an **inflorescence**. The inflorescence is the plumelike structure that you see on sugarcane or the spike of a wheat plant. Corn is a special case, both the cob and the tassel are inflorescences, but the cob has only female flowers and the tassel only male. Some other grasses have separate male and female inflorescences and many have some of the spikelets with only male flowers, while other spikelets in the same inflorescence have hermaphrodite flowers. The grasses also have a very characteristic fruit (grain) called a caryopsis, which consists of the ovary with one or more of the floret bracts attached.

inflorescence an arrangement of flowers on a stalk

Pollination and Dispersal

Most grasses are wind-pollinated. Their anthers are versatile, meaning that they pivot on their stalk (or **filament**), and the stalks are very flexible, like a piece of string. At the appropriate time, usually early in the morning, the lodicules will swell with water and push the lemma and palea apart. The anthers will then pop out of the flower and dangle in the wind on their filaments, releasing their pollen as the breeze jostles them during the day. Most grass pollen is perfectly smooth and round with a single small hole in it. This is characteristic of many wind-pollinated plants. A few grasses—especially those that grow deep in the rain forest—are pollinated by insects, probably because there is no wind. Grasses have a myriad of dispersal mechanisms for their seeds. Some rain forest grasses shoot their seeds several feet across the forest floor and others have flowers that bloom underground on the tips of long rhizomes and may have an association with ants. Many grasses have smooth fruits that get blown by wind or carried either inside

filament a threadlike extension

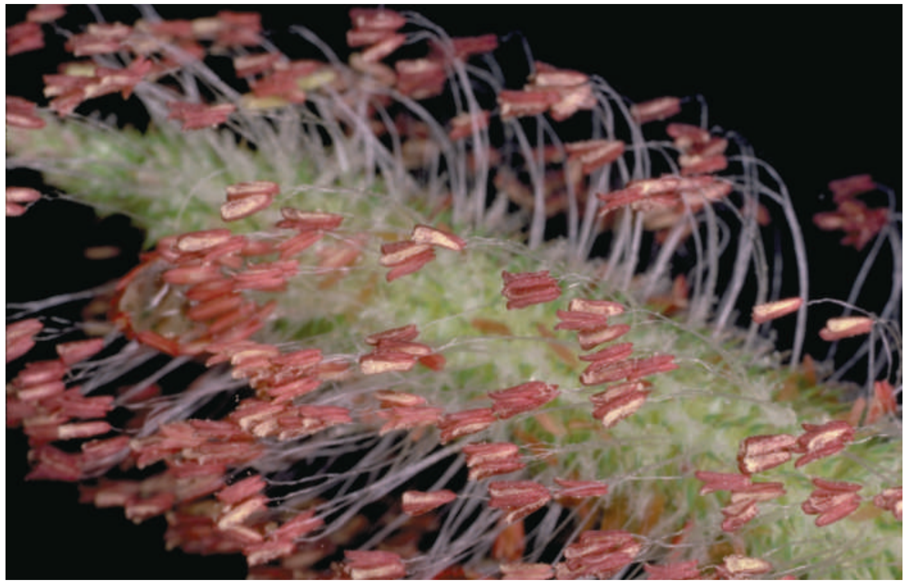
GRASSES CULTIVATED FOR FOOD

Common Name	Scientific Name	Geographic Origin and Area of Domestication	Area of Cultivation
Wheat	*Triticum aestivum*	Southwest Asia, especially Turkey and environs	Worldwide in temperate areas, especially in the Western Hemisphere
Maize or Corn	*Zea mays*	Mexico, Guatemala, Honduras	Primarily in the Western Hemisphere in both temperate and tropical areas
Rice	*Oryza sativa*	Asia, probably domesticated in China and southern Asia	Worldwide in mesic to wet tropical and warm temperate areas, especially in Asia
Sugarcane	*Saccharum officinarum*	New Guinea or Indonesia	Worldwide in wet tropical and subtropical areas
Barley	*Hordeum vulgare*	Southwest Asia	Primarily in temperate areas of the Western Hemisphere
Oats	*Avena sativa*	Probably Europe	Primarily in temperate areas of the Western Hemisphere
Rye	*Secale cereale*	Southwest Asia	Primarily in temperate areas of the Western Hemisphere
Millet	Finger millet (*Eleusine coracana*), proso millet (*Panicum miliaceum*), foxtail millet (*Setaria italica*), japanese barnyard millet (*Echinochola crusgalli*), teff millet (*Eragrostis tef*), pearl millet (*Pennisetum* glaucum)*, koda millet* (*Paspalum scrobiculatum*)	Mostly in Europe and North America	Now important for food only in Asia and Africa although widely grown for birdseed in the United States and Europe
Sorghum	*Sorghum bicolor*	Africa	Most important in Africa and other dry regions of the tropics and subtropics

or on the outside of animals. Most have some kind of hooks or hairs to catch passing animals. Many have very specialized fruits that have a hard, drill-like point on one end and one or more long, pinlike awns on the other. An awn can catch the wind and vibrate the point like a jackhammer (e.g., the genus *Aristida*) or they can be twisted and sensitive to moisture (e.g., the genus *Heteropogon*) so that it turns the point like a drill bit into sweaty animal fur or feathers or into the soil. Stiff, back-pointing hairs on the awn and on the hard point of the fruit help by only allowing the fruit to burrow in, not out. Other grass fruits are completely covered with long hairs that allow them to catch the wind and float for several kilometers. Still others have an inflorescence that breaks off and blows across the ground like a tumbleweed unit (e.g., *Eragrostis spectabilis*), or is carried around by birds as nesting material (e.g., *Panicum maximum*). The sandburs (the genus *Cenchrus*) have a spiny bur around their seeds that sticks into your skin or an animal's fur while Job's Tears (*Coix lacryma-jobi*) have a hard, white, shiny flask around the seeds that is used in many tropical regions for beads. Several bamboos have thorns; a very few species of grass have irritating hairs and the leaf edges can be sharp, but other than the high levels of silica found in the leaves of many savanna grasses (which wear down the teeth of grazers), protective structures are rare in the grasses.

Where They Grow

Grasses are not only in your backyard. They are more geographically distributed than any other family of flowering plants. The southernmost recorded flowering plant is the Antarctic hair grass, *Deschampsia antarctica*, and several species of grasses are among the most northern growing tundra


Close-up of grass flower.

plants as well. They are very common in alpine areas and lowlands, in swamps, and in some deserts. When forest is cleared, grasses usually dominate the landscape. They bind the soil and prevent loss of topsoil all over the world. Grasses are planted as cover crops when land is cleared. Taken together, they cover more area on Earth than any other flowering plant family. They are the dominant plant in the savannas that ring Earth at the boundaries of the tropics, and they dominate the boreal steppe (cold temperate grasslands) and the prairies of North America. Tropical savannas currently cover some 23,000,000 square kilometers, or about 20 percent of Earth's land surface. Dominance of grasses in these habitats is usually maintained either because there is not enough water for trees to survive, there is heavy grazing pressure, or because there are fires frequently enough to keep the trees out. Grasses adapted to fire-prone areas have their growing tip either below ground or well protected within a tight clump of leaf bases. When they burn, only the leaves or the old flowerstalks are lost; the growing tip stays safe. They are also generally fast growers; for example, a bamboo has been measured growing 120 centimeters in twenty-four hours. Some grasses are actually stimulated to grow by grazing. The huge herds of more than a hundred different grazing animals in Africa, bison on the great plains of the United States, cattle all over the world, and billions of termites on the savannas of South America are all supported by grass.

There are two major photosynthetic pathways in grasses, C_3 and C_4 (with the exception of the bamboos, which are all $C_{3,}$ and are common in the tropics and some temperate areas of Asia). Almost all grasses at high latitudes are $C_{3,}$ while most of those at the equator are C_4. In general, C_4 grasses can work at higher temperatures and light levels than C_3 grasses but require higher temperatures and/or light levels to begin photosynthesizing.

Economic Importance

The economic importance of grasses can hardly be overstated. They provide the majority of food. Grasses provide much of the starch (e.g., rice, cornmeal, bread, cereal, pasta) and a certain amount of protein, in most human diets. Although a few grasses absorb selenium and other harmful substances from the soil and others have potentially poisonous **cyanogenic** compounds in their shoots and leaves, most are not poisonous. The grains are naturally low in fat and rich in complex carbohydrates. Remember that most livestock eat primarily grass or grass products so leather, wool, meat, and milk also indirectly come from grass. Grasses sweeten what you drink and eat with cane sugar, molasses, and high fructose corn syrup. Corn byproducts also provide the raw material for many chemicals used in industry and everyday life. Grasses provide the raw material for most alcohol products (e.g., sake from rice, rum from sugarcane, beer from barley, bourbon from corn, and other whiskeys from barley, wheat, and rye). Although bamboo shoots are enormously important as a food crop in Asia, the real economic contribution of the bamboos is as a building material and a raw material for paper and furniture. More than three thousand uses have been listed for bamboos in Japan alone. There is even a bamboo culture in Honduras that is based on the giant *Guadua* bamboo. Of course, because corn and rice are the staple foods of many of the world's people, cultures can be defined by them as well. Rice is a sacred plant in many Asian cultures. In contrast to the enormous economic benefit of grasses, it must also be noted that they make up a large percentage of the world's worst weeds, which cost millions of dollars every year to manage. Cogon grass (*Imperata cylindrica*) and Bermuda grass (*Cynodon dactylon*) are two of the most common. Bermuda grass is also the most common grass on Earth. SEE ALSO BAMBOO; CORN; GRAINS; MONOCOTS; PHOTOSYNTHESIS, CARBON FIXATION AND; RICE; SAVANNA; SEED DISPERSAL; WHEAT.

cyanogenic giving rise to cyanide

Gerald F. Guala

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Grasslands

Ecosystems in which grasses and grasslike plants such as sedges and rushes dominate the vegetation are termed grasslands. Grasslands occur on every continent except Antarctica. It is estimated that grasslands once covered as much as 25 to 40 percent of Earth's land surface, but much of this has been plowed and converted to crop production, such as corn, wheat, and soybeans. Prior to the European settlement of North America, the largest continuous grasslands in the United States stretched across the Great Plains from the Rocky Mountains and deserts of the southwestern states to the Mississippi River. Other extensive grasslands are (or were) found in Europe, South America, Asia, and Africa.

ecosystem an ecological community together with its environment

Cattle grazing on grasslands in Spain.

Grasslands can be broadly categorized as temperate or tropical. Temperate grasslands have cold winters and warm-to-hot summers and often have deep fertile soils. Surprisingly, plant growth in temperate grasslands is often nutrient limited because much of the soil nitrogen is stored in forms unavailable for plant uptake. These nutrients, however, are made available to plants when plowing disrupts the structure of the soil. The combination of high soil fertility and relatively gentle topography made grasslands ideal candidates for conversion to crop production. Grasslands in the Midwestern United States that receive the most rainfall (75 to 90 centimeters) and are the most productive are termed tallgrass prairies. Historically, these prairies were most abundant in Iowa, Illinois, Minnesota, and Kansas. The driest grasslands (25 to 35 centimeters of rainfall) and least productive are termed shortgrass prairies or steppes. These grasslands are common in Texas, Colorado, Wyoming, and New Mexico. Grasslands that are intermediate between these extremes are termed midgrass prairies or mixed grass prairies. In tallgrass prairies, the grasses may grow to 3 meters tall in wet years. In shortgrass prairies, grasses seldom grow beyond 25 centimeters in height. In all temperate grasslands, production of root **biomass** belowground exceeds foliage production aboveground. Worldwide, other names for temperate grasslands include steppes, preferred for most of Europe and Asia, veld in Africa, and the pampas in South America. In North America, other names for temperate grasslands include prairies and steppes.

biomass the total dry weight of an organism or group of organisms

Tropical grasslands are warm throughout the year but have pronounced wet and dry seasons. Tropical grassland soils are often less fertile than temperate grassland soils, perhaps due to the high amount of rainfall (50 to 130 centimeters) that falls during the wet season and washes (or leaches) nutrients out of the soil. Most tropical grasslands have a greater density of woody shrubs and trees than temperate grasslands. Some tropical grasslands can be more productive than temperate grasslands. However, other tropical grasslands grow on soils that are quite infertile, or they may be periodically stressed by seasonal flooding. As a result, their productivity is reduced and may be similar to that of temperate grasslands. As noted for temperate grasslands, root production belowground far exceeds foliage production in all tropical grasslands. Other names for tropical grasslands include velds in Africa, and the compos and llanos in South America.

Although temperate and tropical grasslands encompass the most extensive grass-dominated ecosystems, grasses are present in most types of vegetation and regions of the world. Where grasses are locally dominant they may form desert grassland, Mediterranean grassland, **subalpine** and alpine grasslands (sometimes referred to as meadows or parks), and even coastal grassland. Most grasslands are dominated by perennial (long-lived) plants, but there are some annual grasslands in which the dominant species must reestablish each year by seed. Intensively managed, human-planted, and maintained grasslands occur worldwide as well.

subalpine a region less cold or elevated than alpine (mountain top)

It is generally recognized that climate, fire, and grazing are three primary factors that are responsible for the origin, maintenance, and structure of the most extensive natural grasslands. Although these factors will be described separately, their effects are not always independent of each other (e.g., grazing may reduce the fuel available for fire).

Climate

The climate of grasslands is best described as one of extremes. Average temperatures and yearly amounts of rainfall may not be much different from areas that are deserts or forested, but dry periods during which the plants suffer from water stress occur in most years in both temperate and tropical grasslands. The open nature of grasslands is accompanied by the presence of sustained high windspeeds. Windy conditions increase the evaporation of water from grasslands and this increases water stress in the plants and animals. Another factor that increases water stress is the high input of solar radiation in these open ecosystems. This leads to the **convective uplift** of moist air and results in intense thunderstorms. Rain falling in these intense storms may not be effectively captured by the soil, and the subsequent runoff of this water into streams reduces the moisture available to grassland plants and animals. In addition to periods of water stress within the growing season, consecutive years of extreme drought are more common in grassland than in adjacent forested areas. Such droughts may kill even mature trees, but the grasses and other grassland plants have extensive root systems and belowground buds that help them survive and regrow after drought periods.

convective uplift movement of air upwards due to heating from the sun

Fire

Historically, fires were a frequent occurrence in most large grasslands. Most grasslands are not harmed by fire. In fact, many benefit from fire

dormant inactive, not growing

and some depend on fire for their existence. When grasses are **dormant**, the moisture content of the foliage is low and the fine-textured fuel the grasses produce ignites easily and burns rapidly. The characteristic high windspeeds and lack of natural firebreaks in grasslands allows fires to cover large areas quickly. Fires may be started by lightning or set intentionally by humans in both tropical and temperate grasslands. Fires are most common in grasslands with high levels of plant productivity, such as tallgrass prairies, and in these grasslands fire is important for keeping trees and adjacent forests from encroaching into grasslands. Many tree species are killed by fire, or if they are not killed, they are damaged severely because their active growing points are aboveground. Grassland plants survive and even thrive after fire because their buds are belowground, where they are protected from lethal temperatures. In some highly productive grasslands, fire results in an increase in growth of the grasses and a greater production of plant biomass. This occurs because the buildup of dead biomass (mulch) from previous years inhibits growth, and fire removes this mulch layer. However, in drier grasslands, the burning of this dead plant material may cause the soil to become excessively dry due to high evaporation losses. As a result, plants become water-stressed, and growth is reduced after fire.

Most grassland animals are not harmed by fires, particularly if they occur during the dormant season. Animals living belowground are well protected, and most grassland birds and mammals are mobile enough to avoid direct contact with fire. Insects that live in and on the stems and leaves of the plants are the most affected by fire. But these animals have short generation times and populations recover quickly.

Grazing

herbivore an organism that feeds on plant parts

Grazing is a form of herbivory in which most of the plant (leaves aboveground) or specific plant parts (small roots and root hairs belowground) are consumed by **herbivores**. Grazing, both above and belowground, is an important process in all grasslands. Many formerly natural grasslands are now managed for the production of domestic livestock, primarily cattle in North America, as well as sheep in Europe, New Zealand, and other parts of the world.

forb broad-leaved, herbaceous plants

Grazing aboveground by large herbivores alters grasslands in several ways. Grazers remove fuel aboveground and may lessen the frequency and intensity of fires. Most large grazers such as cattle or bison primarily consume the grasses, thus the less-abundant **forb** species may increase in abundance and new species may invade the space that is made available. As a result, plant species diversity may increase in grazed grasslands. However, this effect is strongly dependent on the amount of grazing that occurs. Overgrazing may rapidly degrade grasslands to systems dominated by weedy and nonnative plant species.

Grazers may also accelerate the conversion of plant nutrients from forms that are unavailable for plant uptake to forms that can be readily used. Essential plant nutrients, such as nitrogen, are bound for long periods of time in unavailable (organic) forms in plant foliage, stems, and roots. Microbes slowly decompose these plant parts and the nutrients they contain are only gradually released in available (inorganic) forms. This decomposition process may take more than a year or two. Grazers consume these plant parts and excrete a portion of the nutrients they contain in plant-available forms. This happens very quickly compared to the slow decomposition process, and nutrients are excreted in high concentrations in small patches. Thus, grazers may increase the availability of potentially limiting nutrients to plants as well as alter the spatial distribution of these resources.

Some grasses and grassland plants can compensate for aboveground tissue lost to grazers by growing faster after grazing has occurred. Therefore, even though 50 percent of the grass foliage may be consumed by bison or wildebeest, when compared to ungrazed plants at the end of the season, the grazed grasses may be only slightly smaller, the same size, or even larger. This latter phenomenon, where grazed plants produce more growth than ungrazed plants, is called overcompensation and is somewhat controversial. However, the ability of grasses to compensate or make up partially or completely for foliage lost to grazers is well established. This compensation occurs for several reasons, including an increase in light available to growing shoots in grazed areas, greater nutrient availability (see above) to regrowing plants, and increased water availability. The latter occurs after grazing because the large roots system of the grasses is able to supply abundant water to a relatively small amount of regrowing leaf tissue.

Grassland Biota

By definition, grasses dominate grasslands in terms of plant numbers and biomass, but typically only a few species of grass account for most of the growth. By contrast, both temperate and tropical grasslands contain many more species of forbs than grasses. Forbs can be quite conspicuous when they have brightly colored flowers, and they are very important for maintaining high species diversity (biodiversity) in grasslands. The most conspicuous animals in grasslands are (or were) the large grazers, such as bison and antelope in North America and zebras, gazelles, and wildebeest in Africa. Although it may appear that the large herds of grazers in grasslands consume the most plant biomass, invertebrates such as grasshoppers aboveground can be important consumers of plants in some years, and nematodes and root-feeding invertebrates belowground are actually the most significant consumers of plant biomass.

Insect diversity can be great in grasslands. Even though most of the grasses are wind-pollinated, grassland forbs rely on a wide array of insect species for pollination. Grassland birds are unique in that many nest on the ground and some, such as the burrowing owl, nest belowground. Smaller mammals (e.g., mice, ground squirrels, prairie dogs, gophers) share the subterranean world and burrow extensively in some grasslands. These burrowing mammals may be important consumers of some plant parts and can alter soil nutrient availability to plants.

Conservation and Restoration

In North America, many grasslands are considered endangered ecosystems. For example, in some central Great Plains states that formerly had extensive tall grass prairies, up to 99 percent of these have been plowed and converted to agricultural use or lost due to **urbanization**. Similar but less dramatic losses of mixed and shortgrass prairies have occurred in other

urbanization increase in size or number of cities areas. Because grasslands have tremendous economic value as grazing lands and also serve as critical habitats for many plant and animal species, efforts to conserve the remaining grasslands and restore grasslands on agricultural land are underway in many states and around the world. SEE ALSO BIOME; GRASSES; SAVANNA.

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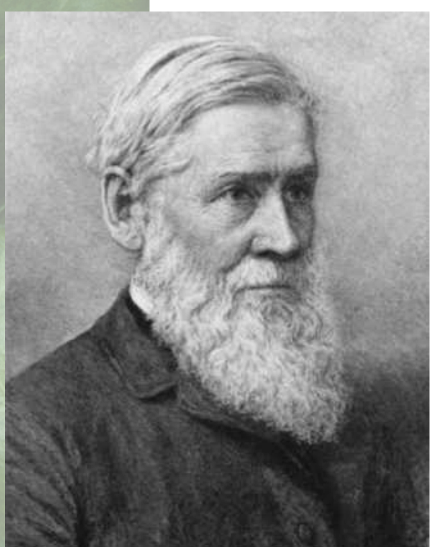
American Botanist
1810–1888



Asa Gray.

floristic related to plants

specimen object or organism under consideration

Asa Gray was the dominant force in botanical science in the United States throughout the mid-nineteenth century. He substantially advanced and influenced the study of North American flora and the dissemination of information about it. Gray's studies led to a reassessment of **floristic** plant geography in North America, and he was famous for the sheer volume of his knowledge and the way he used it to advance American botany. Gray won respect for American botany from abroad. Moreover, he played a critical role in the eventual acceptance of Darwin's theories in the United States.

Asa Gray was born in 1810 in Sauquoit Valley, New York, near Utica. As a youth he helped his father with farm and tannery work. He attended Fairfield Medical School, where he first became acquainted with basic botanical principles. Gray was awarded a medical degree in 1831, but then took a position as an instructor in chemistry, mineralogy, and botany in Utica, thus beginning his career in botany.

Gray corresponded with the famed botanist John Torrey (1796–1873), sending him **specimens** of local plants. In 1833 he joined Torrey in New York, first collecting plants for him, then as his assistant, and then shortly thereafter as his collaborator. Gray had a talent for investigation and scientific description, and even at this early stage of his career he was writing for publication. In 1835 he became curator and librarian at the Lyceum of Natural History in New York. He then accepted a position as botanist of the Wilkes Exploring Expedition, but various delays, coupled with his work on other projects, led to his resignation in 1837 before the expedition even began. Some time after the expedition, Gray was brought in to help publish its scientific results.

Gray began working with Torrey on a comprehensive flora of North America as early as 1835. This project eventually necessitated the study of American specimens located in European herbaria. Also at this time, Gray received a job offer as professor of botany and zoology at the not-yet-opened University of Michigan, and he was assigned the task of travelling to Europe to purchase books and equipment. He consequently went to Europe to study specimens and purchase resources, and while there he met prominent European scientists, including Charles Darwin (1809–1882). In 1839 Gray returned to the United States. Two volumes of the *Flora of North America* were published in 1838 and 1843; a third volume was never completed.

By 1842 the University of Michigan had still not yet opened, and so Gray accepted an invitation to become Fisher Professor of Natural History at Harvard University. In the course of his work and correspondence he built up a large herbarium and library, resources that enabled him to continue his botanical investigations and publications. Many specimens collected by others were given to Gray so that he could study, identify, and, if necessary, name them, publishing their descriptions and expanding botanical knowledge.

Gray published prolifically, including major studies such as the *Manual of the Botany of the Northern United States* (1848), the *Genera Florae Americae Boreali-Orientalis Illustrata* (1848–49), and various reports on botanical findings from expeditions and surveys. He also wrote a number of popular textbooks, held in high esteem by his peers and used widely in preparatory schools and colleges. These included *Elements of Botany* (1836), *First Lessons in Botany and Vegetable Physiology* (1857), and *How Plants Grow* (1858). He published two parts of a *Synoptical Flora of North America* before he died, and two more parts were published later by others.

The Flora of North America

Gray maintained an intense interest in the flora of North America throughout his career. This interest was fueled by various plant collection efforts, particularly in the American West, conducted as a result of mapping and surveying being done for the railroads and the geological surveys. Collectors also accompanied military expeditions, bringing back specimens from farther afield. Several new scientific institutions were formed, in part to accommodate the data and specimens being gathered.

Collectors brought new species to the attention of both Torrey and Gray, who influenced where plants were being collected and how the resulting information was processed and disseminated. Gray's extensive studies of collected specimens gave him an unparalleled working understanding of the North American landscape and the plants within it, including their distribution.

Evolution and Plant Geography

Gray also studied specimens collected from elsewhere, and he eventually demonstrated a direct relationship between certain Japanese and eastern North American plants. Many of the same species were found in both places but not elsewhere. Gray argued for a common ancestry for these species, reasoning that they must have grown all the way across the northern continent at some time in the distant past, and that glaciers during the ice ages wiped out large sections of growth, so that the now-separated plants developed different characteristics. In 1859, this work led to a reassessment of plant geography in North America.

Gray expressed these ideas to Darwin, who also shared his own ideas with Gray before publishing them in *On the Origin of Species* in the same year. Gray became an advocate for Darwin's theories in the United States, helping to move the American scientific establishment further away from Linnaean ideas and toward those of Darwin. He demonstrated to scientists abroad that botany in North America was now being pursued with a professionalism comparable to that found in Europe. Gray was also a factor in the enhancement of scientific infrastructure in the United States, building an herbarium and library, influencing expeditions, and advising museums. These developments would persuade American collectors to entrust specimens to American institutions rather than sending them abroad to the great herbaria of Europe. Botany in the United States came of age with the work of Asa Gray. Gray received many honors during his lifetime and was a member of numerous academies and scholarly societies in America and Europe. He died in Cambridge, Massachusetts, in 1888. SEE ALSO FLORA; HERBARIA; TAXONOMIST; TAXONOMY; TAXONOMY, HISTORY OF; TORREY, JOHN.

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Greenhouse Effect ***See Global Warming.***

Green Revolution

Green revolution refers to the breeding and widespread use of new varieties of cereal grains, especially wheat and rice. These semidwarf varieties boost yields when grown with high inputs of fertilizer and water. Green revolution agriculture became widespread in less-industrialized countries in the 1960s when international aid agencies sponsored scientific and educational projects promoting the green revolution. These programs—including the adoption of new wheat varieties in India and Pakistan and new rice varieties in the Philippines and Indonesia—supported foreign policy objectives of the United States and were intended to alleviate hunger.

Supporters noted that the green revolution increased crop yields. India, for example, produced more wheat and rice, which helped avoid famines and save foreign exchange currency. Critics, however, charged that the green revolution increased inequalities: rich farmers became richer and poor farmers became poorer. Critics also complained that the green revolution encouraged increased environmental problems through the use of fertilizers, pesticides, and irrigation.

There were problems with both perspectives on the green revolution policies. Critics avoided providing realistic alternatives for solving national food deficits, and supporters avoided noting that poor individuals continued to be hungry, despite the increased supplies.

The green revolution was a change in agricultural practices with secondary social and political effects. Both industrialized and less-industrialized countries adopted the practices. Almost all wheat and rice grown today originated in the green revolution. SEE ALSO BORLAUG, NORMAN; ECONOMIC IMPORTANCE OF PLANTS; FERTILIZER; GRAINS; RICE; WHEAT.

John H. Perkins

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Gymnosperms

Gymnosperms are seed plants that do not produce flowers. The term *gymnosperm* means "naked seed." However, usually when the seeds of gymnosperms are immature they are enclosed within and protected by modified leaves or a cone. In flowering plants (or *angiosperms*, which means "vessel seed") the ovary wall or fruit encloses the seeds, whereas in gymnosperms there is no equivalent structure; hence, the interpretation of the seeds as "naked" or not enclosed.

There are four groups of gymnosperms living today—Coniferophyta, Cycadophyta, Ginkgophyta, and Gnetophyta—but many additional groups are known from the fossil record. Seed plants evolved more than 350 million years ago and the first seed plants were gymnosperms. The relationship of the flowering plants to the gymnospermous seed plants remains a hotly contested issue within the scientific community.

Although each group of gymnosperms has its own specific characteristics, some features are shared throughout. For example, all gymnosperms produce at least some secondary growth, whereas secondary growth is lacking from most spore-bearing (nonseed) plants. Secondary growth is plant growth that does not occur directly from the tips of the plant; it is growth that occurs horizontally (or radially) rather than vertically. The most abundant product of secondary growth is the secondary xylem (xylem is the water-conducting tissue of plants), or wood.

Aspects of reproduction are also shared by all the gymnosperms. The ovule (the technical term for the seed prior to fertilization) consists of female nutritive tissue plus the female gamete, or egg, both enclosed by a

DISTINGUISHING CHARACTERS OF GYMNOSPERMS

Characters	Coniferophyta	Cycadophyta	Ginkgophyta	Gnetophyta
Extant members	50–60 genera, about 550 species	11 genera, about 160 species	1 species (*Ginkgo biloba*)	3 genera: *Ephedra* (35 species), *Gnetum* (30 species), *Welwitschia* (1 species)
Distribution	Worldwide, especially temperate regions	Tropics	Native to a small area of China	Isolated areas of temperate and tropical regions
Habit	Trees with branched woody trunk	Trees with unbranched fleshy trunk	Trees with branched woody trunk	Shrubs, vines, small trees, or weird tubers
Leaves	Simple, needlelike or broad	Large, compound (each leaf composed of many leaflets)	Simple, fan-shaped	Simple, needlelike or broad
Reproductive structure	Simple (unbranched) male, compound (branched) female cones	Simple cones (unbranched), male or female	Simple cones (unbranched), male or female	Compound (branched) male or female cones
Sex	Separate male and female cones on each plant (monoecious) or separate male and female plants (dioecious)	Individual plant male or female (dioecious)	Individual plant male or female (dioecious)	Individual plant male or female (dioecious)
Seeds	Small, without differentiated layers	Large, with outer fleshy layer and middle stony layer	Large, with outer fleshy layer and middle stony layer	Small, without differentiated layers
Sperm	No flagella; pollen tube delivers to egg	Swims using many flagella	Swims using many flagella	No flagella; pollen tube delivers to egg

layer of protective tissue (the integument). The male gamete is carried within the pollen. In most gymnosperms pollen is produced in great amounts, and the pollen grains are dispersed by the wind. Usually a small amount of sticky liquid (the pollination drop) is exuded at the tip of the ovule. Pollen grains become stuck in the pollination drop and, as the drop dries, the pollen is pulled into the ovule. Depending on the type of gymnosperm, the male gamete is released from the pollen and swims to the egg, or the male gamete is transported within a tube that grows to the egg. The fertilized egg then develops into the embryo of the seed. Ultimately, when the seed germinates, the embryo grows to produce the young seedling using the female nutritive tissue as a source of energy. An unusual attribute of the gymnosperms, except for the gnetophytes, is the long length of time—a year or more—that passes between the production of the egg and the sperm and the actual occurrence of fertilization.

Coniferophyta

The Coniferophyta, or conifers, are the most abundant group of living gymnosperms and the first of the living gymnosperm groups to appear in the fossil record. They have been important components of Earth's vegetation for almost three hundred million years. The oldest (bristlecone pine), the tallest (coast redwood), and the biggest (giant sequoia) organisms on the planet today are conifers. Most conifers are large trees that make abundant wood, have small evergreen leaves, and produce their seeds within woody cones.

Although most conifers fit that standard description, there are numerous exceptions. First, not all conifers are evergreen. A few types, such as the larch, are deciduous, losing all their leaves each fall and growing new leaves

The female cones produced by most conifers are complex structures made of repeating units.

in the spring. Even the leaves of the evergreen type are not immortal; it is just that the senescence (aging and death) of leaves occurs individually rather than all at once. Second, not all conifers have small or needlelike leaves. Some conifers, native to the Southern Hemisphere, have broad leaves. Third, although all conifers are woody plants, not all conifers are large trees. A number are shrubs or small trees, and one is even a parasite on the roots of other coniferous trees. Finally, not all conifers have cones as people usually think of them. Some conifers, such as the yew, have solitary seeds covered with a fleshy, colorful tissue.

The female cones produced by most conifers are complex structures that are made of repeating units, each consisting of ovules on a woody platform (ovuliferous scale) beneath which is a bract (e.g., the "mouse tail" that peeks out of Douglas-fir cones). Cones of the other gymnosperms lack the equivalent of the ovuliferous scale. Conifers make rather small ovules and lack swimming sperm.

Cycadophyta

The Cycadophyta, or cycads, are restricted to tropical latitudes and were more abundant in the geologic past. These plants have unbranched, fleshy stems. The trunks of some species can grow fairly tall (15 to 18 meters), but all cycads lack extensive wood development. Because so much water is present in the stems, the plants are very vulnerable to damage from freezing (think of a soda can that explodes after you forget you have placed it in the freezer). Thus the cycads are restricted to parts of the world where freezing temperatures are rare or absent. A few types are found naturally in subtropical areas where mild freezing temperatures occasionally occur; these types of cycads have short, squat, subterranean stems. Some additional cycad species are hardy as ornamentals in similar subtropical to warm temperate areas. Excellent outdoor collections of cycads can be seen in the United States at Fairchild Botanical Garden in Miami, Florida, or at Huntington Botanical Garden east of Los Angeles, California.

A cycad, a gymnosperm that was more abundant in the geologic past.

The leaves of cycads occur as a crown at the top of the stem. Most often the leaves are very large (up to 1.5 meters in length), leathery, and compound; that is, the blade of the leaf is made of many separate leaflets. When the leaves fall off, usually the base of the leaf remains attached to the stem. Thus, the trunk is protected from herbivory and to some extent from freezing by the remnant bases.

Individual cycad plants are either male or female. At the tip of the trunk within the crown of leaves a cone develops that will either contain pollen or ovules, depending on the sex of the plant. Cycads make very large ovules and swimming sperm.

Ginkgophyta

Only one species of the Ginkgophyta group remains living today: the maidenhair tree, *Ginkgo biloba.* Twenty to thirty million years ago the ancestor of the modern species was found throughout the Northern Hemisphere. However, climatic changes have led to the plants gradually becoming reduced to a smaller and smaller territory. Since the last ice age, wild populations have been restricted to a small area in China. It is debated whether or not any populations are truly wild. The tree still exists today because it was a sacred plant maintained in monasteries. Now the ginkgo tree is commonly used as a street tree and so has regained, in some sense, much of its earlier territory. Individual plants can live very long lives (more than one thousand years), and the species is unusually resistant to pollution and disease. The *Ginkgo* plant is a fairly tall (25 meters or more), much-branched tree with abundant wood, bearing fan-shaped leaves.

Individual ginkgo trees are either male or female. The sex of the plant does not become apparent until the tree is fifteen to twenty years old. Male plants are preferred as ornamentals. The ovule produced by the female is large with a stony interior and a fleshy outer covering that produces a smell usually equated with rotting butter. Ginkgo also produces swimming sperm.

Gnetophyta

The Gnetophyta are a small, odd group of living gymnosperms. Three types are known, each being somewhat different from the other gnetophytes and unusual among the seed plants in its own way. Species of the genus *Ephedra* are shrubby plants of arid temperate regions. They have tiny leaves and the stems are often green and photosynthetic. Species of the genus *Gnetum* are tropical plants that are small trees or, more usually, vines. The gnetums are unusual among the gymnosperms in that they produce broad leaves with netted venation similar to that found in flowering plants. The third group is represented by a single species, *Welwitschia mirabilis*. *Welwitschia* has been described as the "weirdest plant on Earth," a plant that has "lost its head" or a giant seedling that can reproduce. *Welwitschia* is native to the Namib Desert of southwest Africa and consists of a large tuber or taproot and two long, strap-shaped leaves that grow from their bases and are retained for the life of the plant.

Most gnetophytes produce separate female and male cones born on separate (male or female) plants. Each type of gnetophyte has a slightly different reproductive structure but all are variations on one theme: pairs of papery bracts (modified leaves) surround the ovule or pollen organs. Some botanists compare these bracts to the petals and **sepals** of angiosperm flowers, whereas others equate them to components of the cone found in conifers. Other aspects of the gnetophyte **morphology** are also ambiguous and, depending on their interpretation, suggests an evolutionary link to either the conifers or the angiosperms. For example, vessels, specialized water-conducting cells, occur in the wood of gnetophytes. These cells are dead at maturity, empty of any contents. Vessels lack any end walls; they are open-ended tubes that line up end to end and act as a pipe to transport water without any obstructions. Most flowering plants have vessels but most other types of plants lack this cell type. Some plant scientists see the gnetophyte vessels as evidence that gnetophytes and angiosperms share a common ancestor. However, because of differences in vessel cell anatomy and development between gnetophytes and flowering plants, other botanists consider the gnetophyte vessel to be an independent evolution of a water transport cell that lost an end wall. Molecular comparisons of the seed plants using different types of deoxyribonucleic acid (DNA) data have not settled this debate: gnetophytes remain a problematic group in terms of evolutionary placement and morphological interpretation.

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

morphology shape and form

Ecological Significance

Conifers are the gymnospermous group with the most profound ecological role in Earth's vegetation. Conifers dominate some vegetation types, such as the taiga of high northern latitudes or boreal forests of lower latitudes. Some temperate forests, for example in Argentina, Australia, or northwestern North America, are also composed almost exclusively of coniferous trees.

Conifers can also be important as successional species or as the climax vegetation of odd environments in other temperate or tropical areas. For example, in environments prone to fire, with a long enough growing season and enough precipitation to support the growth of trees, conifers are often present. Conifer bark is thicker than most flowering plant tree bark and so coniferous trees are better able to survive ground fires. Some conifer cones open to release their seeds only after a fire.

Economic Significance

Conifers are also considered the most important gymnospermous group from an economic perspective. Coniferous trees are a very important source of timber for lumber and paper. They are harvested in North America, parts of Europe and Asia, and in Australia. In addition to timber, conifers provide Christmas trees, ornamental trees and shrubs, turpentine, and resin. Pine nuts (or pignoli), the seeds of some pine trees, are used as food. An important cancer-fighting drug, taxol, has been derived from the bark and leaves of the Pacific Coast yew (*Taxus*). Other gymnosperms also are the source of drugs and herbal medications. The powerful stimulant ephedrine derived from the gnetophyte Ephedra is often used in cold and allergy medications, and **compounds** shown to improve the mental capacities of the elderly have been discovered in *Ginkgo*. Ginkgo seeds are also quite nutritious and are used as food in Asia. Ginkgo and cycads are also important as ornamentals. SEE ALSO CONIFEROUS FORESTS; CONIFERS; EVOLUTION OF PLANTS; GINKGO; RECORD-HOLDING PLANTS; TREES; WOOD PRODUCTS.

Linda A. Raubeson

compound a substance formed from two or more elements

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Glossary

abiotic nonliving

abrade to wear away through contact

abrasive tending to wear away through contact

abscission dropping off or separating

accession a plant that has been acquired and catalogued

achene a small, dry, thin-walled type of fruit

actinomycetes common name for a group of Gram-positive bacteria that are filamentous and superficially similar to fungi

addictive capable of causing addiction or chemical dependence

adhesion sticking to the surface of

adventitious arising from secondary buds, or arising in an unusual position

aeration the introduction of air

albuminous gelatinous, or composed of the protein albumin

alkali chemically basic; the opposite of acidic

alkalinization increase in basicity or reduction in acidity

alkaloid bitter secondary plant compound, often used for defense

allele one form of a gene

allelopathy harmful action by one plant against another

allopolyploidy a polyploid organism formed by hybridization between two different species or varieties (*allo* = other)

alluvial plain broad area formed by the deposit of river sediment at its outlet

amended soils soils to which fertilizers or other growth aids have been added

amendment additive

anaerobic without oxygen

analgesic pain-relieving

analog a structure or thing, especially a chemical, similar to something else

angiosperm a flowering plant

anomalous unusual or out of place

anoxic without oxygen

antenna system a collection of protein complexes that harvests light energy and converts it to excitation energy that can migrate to a reaction center; the light is absorbed by pigment molecules (e.g., chlorophyll, carotenoids, phycobilin) that are attached to the protein

anthropogenic human-made; related to or produced by the influence of humans on nature

antibodies proteins produced to fight infection

antioxidant a substance that prevents damage from oxygen or other reactive substances

apical meristem region of dividing cells at the tips of growing plants

apical at the tip

apomixis asexual reproduction that may mimic sexual reproduction

appendages parts that are attached to a central stalk or axis

arable able to be cultivated for crops

Arcto-Tertiary geoflora the fossil flora discovered in Arctic areas dating back to the Tertiary period; this group contains magnolias (*Magnolia*), tulip trees (*Liriodendron*), maples (*Acer*), beech (*Fagus*), black gum (*Nyssa*), sweet gum (*Liquidambar*), dawn redwood (*Metasequoia*), cypress (*Taxodium*), and many other species

artifacts pots, tools, or other cultural objects

assayer one who performs chemical tests to determine the composition of a substance

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

attractant something that attracts

autotroph "self-feeder"; any organism that uses sunlight or chemical energy

auxin a plant hormone

avian related to birds

axil the angle or crotch where a leaf stalk meets the stem

axillary bud the bud that forms in the angle between the stem and leaf

basipetal toward the base

belladonna the source of atropine; means "beautiful woman," and is so named because dilated pupils were thought to enhance a woman's beauty

binomial two-part

biodirected assays tests that examine some biological property

biodiversity degree of variety of life

biogeography the study of the reasons for the geographic distribution of organisms

biomass the total dry weight of an organism or group of organisms

biosphere the region of the Earth in which life exists

biosynthesis creation through biological pathways

biota the sum total of living organisms in a region of a given size

biotic involving or related to life

bryologist someone who studies bryophytes, a division of nonflowering plants

campanulate bell-shaped

capitulum the head of a compound flower, such as a dandelion

cardiotonic changing the contraction properties of the heart

carotenoid a yellow-colored molecule made by plants

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

catastrophism the geologic doctrine that sudden, violent changes mark the geologic history of Earth

cation positively charged particle

catkin a flowering structure used for wind pollination

centrifugation spinning at high speed in a centrifuge to separate components

chitin a cellulose-like molecule found in the cell wall of many fungi and arthropods

chloroplast the photosynthetic organelle of plants and algae

circadian "about a day"; related to a day

circumscription the definition of the boundaries surrounding an object or an idea

cisterna a fluid-containing sac or space

clade a group of organisms composed of an ancestor and all of its descendants

cladode a modified stem having the appearance and function of a leaf

coalescing roots roots that grow together

coleoptile the growing tip of a monocot seedling

collenchyma one of three cell types in ground tissue

colonize to inhabit a new area

colony a group of organisms inhabiting a particular area, especially organisms descended from a common ancestor

commensalism a symbiotic association in which one organism benefits while the other is unaffected

commodities goods that are traded, especially agricultural goods

community a group of organisms of different species living in a region

compaction compacting of soil, leading to the loss of air spaces

complex hybrid hybridized plant having more than two parent plants

compound a substance formed from two or more elements

concentration gradient a difference in concentration between two areas

continental drift the movement of continental land masses due to plate tectonics

contractile capable of contracting

convective uplift the movement of air upwards due to heating from the sun

coppice growth the growth of many stems from a single trunk or root, following the removal of the main stem

cortical relating to the cortex of a plant

covalent held together by electron-sharing bonds

crassulacean acid metabolism water-conserving strategy used by several types of plants

crop rotation alternating crops from year to year in a particular field

cultivation growth of plants, or turning the soil for growth of crop plants

crystallography the use of x-rays on crystals to determine molecular structure

cuticle the waxy outer coating of a leaf or other structure, which provides protection against predators, infection, and water loss

cyanide heap leach gold mining a technique used to extract gold by treating ore with cyanide

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

cyanogenic giving rise to cyanide

cytologist a scientist who studies cells

cytology the microscopic study of cells and cell structure

cytosol the fluid portion of a cell

cytostatic inhibiting cell division

deductive reasoning from facts to conclusion

dendrochronologist a scientist who uses tree rings to determine climate or other features of the past

dermatophytes fungi that cause skin diseases

desertification degradation of dry lands, reducing productivity

desiccation drying out

detritus material from decaying organisms

diatoms hard-shelled, single-celled marine organisms; a type of algae

dictyosome any one of the membranous or vesicular structures making up the Golgi apparatus

dioicous having male and female sexual parts on different plants

diploid having two sets of chromosomes, versus having one set (haploid)

dissipate to reduce by spreading out or scattering

distal further away from

diurnal daily, or by day

domestication the taming of an organism to live with and be of use to humans

dormant inactive, not growing

drupe a fruit with a leathery or stone-like seed

dynamical system theory the mathematical theory of change within a system

ecophysiological related to how an organism's physiology affects its function in an ecosystem

ecosystem an ecological community and its environment

elater an elongated, thickened filament

empirical formula the simplest whole number ratio of atoms in a compound

emulsifier a chemical used to suspend oils in water

encroachment moving in on

endemic belonging or native to a particular area or country

endophyte a fungus that lives within a plant

endoplasmic reticulum the membrane network inside a cell

endosperm the nutritive tissue in a seed, formed by the fertilization of a diploid egg tissue by a sperm from pollen

endosporic the formation of a gametophyte inside the spore wall

endosymbiosis a symbiosis in which one organism lives inside the other

Enlightenment eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

entomologist a scientist who studies insects

enzyme a protein that controls a reaction in a cell

ephemeral short-lived

epicuticle the waxy outer covering of a plant, produced by the epidermis

epidermis outer layer of cells

epiphytes plants that grow on other plants

escarpment a steep slope or cliff resulting from erosion

ethnobotanist a scientist who interacts with native peoples to learn more about the plants of a region

ethnobotany the study of traditional uses of plants within a culture

euglossine bees a group of bees that pollinate orchids and other rain-forest plants

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

extrafloral outside the flower

exudation the release of a liquid substance; oozing

facultative capable of but not obligated to

fertigation application of small amounts of fertilizer while irrigating

filament a threadlike extension

filamentous thin and long

flagella threadlike extension of the cell membrane, used for movement

flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

florigen a substance that promotes flowering

floristic related to plants

follicle sac or pouch

forbs broad-leaved, herbaceous plants

free radicals toxic molecular fragments

frugivous feeding on fruits

gametangia structure where gametes are formed

gametophyte the haploid organism in the life cycle

gel electrophoresis a technique for separating molecules based on size and electrical charge

genera plural of genus; a taxonomic level above species

genome the genetic material of an organism

genotype the genetic makeup of an organism

germplasm hereditary material, especially stored seed or other embryonic forms

globose rounded and swollen; globe-shaped

gradient difference in concentration between two places

green manure crop planted to be plowed under to nourish the soil, especially with nitrogen

gymnosperm a major group of plants that includes the conifers

gynoecium the female reproductive organs as a whole

gypsipherous containing the mineral gypsum

hallucinogenic capable of inducing hallucinations

haploid having one set of chromosomes, versus having two (diploid)

haustorial related to a haustorium, or food-absorbing organ

hemiterpene a half terpene

herbivore an organism that feeds on plant parts

heterocyclic a chemical ring structure composed of more than one type of atom, for instance carbon and nitrogen

heterosporous bearing spores of two types, large megaspores and small microspores

heterostylous having styles (female flower parts) of different lengths, to aid cross-pollination

heterotroph an organism that derives its energy from consuming other organisms or their body parts

holistic including all the parts or factors that relate to an object or idea

homeotic relating to or being a gene that produces a shift in structural development

homology a similarity in structure between anatomical parts due to descent from a common ancestor

humus the organic material in soil formed from decaying organisms

hybrid a mix of two varieties or species

hybridization formation of a new individual from parents of different species or varieties

hydrological cycle the movement of water through the biosphere

hydrophobic water repellent

hydroponic growing without soil, in a watery medium

hydroxyl the chemical group -OH

hyphae the threadlike body mass of a fungus

illicit illegal

impede to slow down or inhibit

inert incapable of reaction

inflorescence a group of flowers or arrangement of flowers in a flower head

infrastructure roads, phone lines, and other utilities that allow commerce

insectivorous insect-eating

intercalary inserted; between

interspecific hybridization hybridization between two species

intertidal between the lines of high and low tide

intracellular bacteria bacteria that live inside other cells

intraspecific taxa levels of classification below the species level

intuiting using intuition

ionic present as a charged particle

ions charged particles

irreversible unable to be reversed

juxtaposition contrast brought on by close positioning

lacerate cut

Lamarckian inheritance the hypothesis that acquired characteristics can be inherited

lamellae thin layers or plate-like structure

land-grant university a state university given land by the federal government on the condition that it offer courses in agriculture

landrace a variety of a cultivated plant, occurring in a particular region

lateral to the side of

legume beans and other members of the Fabaceae family

lignified composed of lignin, a tough and resistant plant compound

lineage ancestry; the line of evolutionary descent of an organism

loci (singular: locus) sites or locations

lodging falling over while still growing

lytic breaking apart by the action of enzymes

macromolecule a large molecule such as a protein, fat, nucleic acid, or carbohydrate

macroscopic large, visible

medulla middle part

megaphylls large leaves having many veins or a highly branched vein system

meiosis the division of chromosomes in which the resulting cells have half the original number of chromosomes

meristem the growing tip of a plant

mesic of medium wetness

microfibrils microscopic fibers in a cell

micron one millionth of a meter; also called micrometer

microphylls small leaves having a single unbranched vein

mitigation reduction of amount or effect

mitochondria cell organelles that produce adenosine triphosphate (ATP) to power cell reactions

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

molecular systematics the analysis of DNA and other molecules to determine evolutionary relationships

monoculture a large stand of a single crop species

monomer a single unit of a multi-unit structure

monophyletic a group that includes an ancestral species and all its descendants

montane growing in a mountainous region

morphology shape and form

motile capable of movement

mucilaginous sticky or gummy

murein a peptidoglycan, a molecule made up of sugar derivatives and amino acids

mutualism a symbiosis between two organisms in which both benefit

mycelium the vegetative body of a fungus, made up of threadlike hyphae

$NADP^+$ oxidized form of nicotinamide adenine dinucleotide phosphate

NADPH reduced form of nicotinamide adenine dinucleotide phosphate, a small, water-soluble molecule that acts as a hydrogen carrier in biochemical reactions

nanometer one billionth of a meter

nectaries organs in flowers that secrete nectar

negative feedback a process by which an increase in some variable causes a response that leads to a decrease in that variable

neuromuscular junction the place on the muscle surface where the muscle receives stimulus from the nervous system

neurotransmitter a chemical that passes messages between nerve cells

node branching site on a stem

nomenclature a naming system

nonmotile not moving

nonpolar not directed along the root-shoot axis, or not marked by separation of charge (unlike water and other polar substances)

nonsecretory not involved in secretion, or the release of materials

Northern Blot a technique for separating RNA molecules by electrophoresis and then identifying a target fragment with a DNA probe

nucleolar related to the nucleolus, a distinct region in the nucleus

nurseryman a worker in a plant nursery

obligate required, without another option

obligate parasite a parasite without a free-living stage in the life cycle

odorant a molecule with an odor

organelle a membrane-bound structure within a cell

osmosis the movement of water across a membrane to a region of high solute concentration

oviposition egg-laying

oxidation reaction with oxygen, or loss of electrons in a chemical reaction

paleobotany the study of ancient plants and plant communities

pangenesis the belief that acquired traits can be inherited by bodily influences on the reproductive cells

panicle a type of inflorescence (flower cluster) that is loosely packed and irregularly branched

paraphyletic group a taxonomic group that excludes one or more descendants of a common ancestor

parenchyma one of three types of cells found in ground tissue

pastoralists farming people who keep animal flocks

pathogen disease-causing organism

pedicel a plant stalk that supports a fruiting or spore-bearing organ

pentamerous composed of five parts

percolate to move through, as a fluid through a solid

peribacteroid a membrane surrounding individual or groups of rhizobia bacteria within the root cells of their host; in such situations the bacteria

have frequently undergone some change in surface chemistry and are referred to as bacteroids

pericycle cell layer between the conducting tissue and the endodermis

permeability the property of being permeable, or open to the passage of other substances

petiole the stalk of a leaf, by which it attaches to the stem

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral. Low pH numbers indicate high acidity while high numbers indicate alkalinity

pharmacognosy the study of drugs derived from natural products

pharmacopeia a group of medicines

phenology seasonal or other time-related aspects of an organism's life

pheromone a chemical released by one organism to influence the behavior of another

photooxidize to react with oxygen under the influence of sunlight

photoperiod the period in which an organism is exposed to light or is sensitive to light exposure, causing flowering or other light-sensitive changes

photoprotectant molecules that protect against damage by sunlight

phylogenetic related to phylogeny, the evolutionary development of a species

physiology the biochemical processes carried out by an organism

phytogeographer a scientist who studies the distribution of plants

pigments colored molecules

pistil the female reproductive organ of a flower

plasmodesmata cell-cell junctions that allow passage of small molecules between cells

polyculture mixed species

polyhedral in the form of a polyhedron, a solid whose sides are polygons

polymer a large molecule made from many similar parts

polynomial "many-named"; a name composed of several individual parts

polyploidy having multiple sets of chromosomes

polysaccharide a linked chain of many sugar molecules

population a group of organisms of a single species that exist in the same region and interbreed

porosity openness

positive feedback a process by which an increase in some variable causes a response that leads to a further increase in that variable

precipitation rainfall; or the process of a substance separating from a solution

pre-Columbian before Columbus

precursor a substance from which another is made

predation the act of preying upon; consuming for food

primordial primitive or early

progenitor parent or ancestor

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

propagate to create more of through sexual or asexual reproduction

protist a usually single-celled organism with a cell nucleus, of the kingdom Protista

protoplasmic related to the protoplasm, cell material within the cell wall

protoplast the portion of a cell within the cell wall

psychoactive causing an effect on the brain

pubescence covered with short hairs

pyruvic acid a three-carbon compound that forms an important intermediate in many cellular processes

quadruple hybrid hybridized plant with four parents

quantitative numerical, especially as derived from measurement

quid a wad for chewing

quinone chemical compound found in plants, often used in making dyes

radii distance across, especially across a circle (singular = radius)

radioisotopes radioactive forms of an element

rambling habit growing without obvious intended direction

reaction center a protein complex that uses light energy to create a stable charge separation by transferring a single electron energetically uphill from a donor molecule to an acceptor molecule, both of which are located in the reaction center

redox oxidation and reduction

regurgitant material brought up from the stomach

Renaissance a period of artistic and intellectual expansion in Europe from the fourteenth to the sixteenth century

salinization increase in salt content

samara a winged seed

saprophytes plants that feed on decaying parts of other plants

saturated containing as much dissolved substance as possible

sclerenchyma one of three cell types in ground tissue

sedimentation deposit of mud, sand, shell, or other material

semidwarf a variety that is intermediate in size between dwarf and full-size varieties

senescent aging or dying

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

sequester to remove from circulation; lock up

serology the study of serum, the liquid, noncellular portion of blood

seta a stiff hair or bristle

silage livestock food produced by fermentation in a silo

siliceous composed of silica, a mineral

silicified composed of silicate minerals

soil horizon distinct layers of soil

solute a substance dissolved in a solution

Southern blot a technique for separating DNA fragments by electrophoresis and then identifying a target fragment with a DNA probe

spasticity abnormal muscle activity caused by damage to the nerve pathways controlling movement

speciation the creation of new species

specimen an object or organism under consideration

speciose marked by many species

sporophyte the diploid, spore-producing individual in the plant life cycle

sporulate to produce or release spores

sterile not capable or involved in reproduction, or unable to support life

sterols chemicals related to steroid hormones

stolons underground stems that may sprout and form new individuals

stomata openings between guard cells on the underside of leaves that allow gas exchange

stratification layering, or separation in space

stratigraphic geology the study of rock layers

stratigraphy the analysis of strata (layered rock)

strobili cone-like reproductive structures

subalpine a region less cold or elevated than alpine (mountaintop)

substrate the physical structure to which an organism attaches, or a molecule acted on by enzymes

succession the pattern of changes in plant species that occurs after a soil disturbance

succulent fleshy, moist

suckers naturally occuring adventitious shoots

suffrutescent a shrub-like plant with a woody base

sulfate a negatively charged particle combining sulfur and oxygen

surfaced smoothed for examination

susceptibility vulnerability

suture line of attachment

swidden agriculture the practice of farming an area until the soil has been depleted and then moving on

symbiont one member of a symbiotic association

symbiosis a relationship between organisms of two different species in which at least one benefits

systematists scientists who study systematics, the classification of species to reflect evolutionary relationships

systemic spread throughout the plant

tannins compounds produced by plants that usually serve protective functions, often colored and used for "tanning" and dyeing

taxa a type of organism, or a level of classification of organisms

tensile forces forces causing tension, or pulling apart; the opposite of compression

tepal an undifferentiated sepal or petal

Tertiary period geologic period from sixty-five to five million years ago

tetraploid having four sets of chromosomes; a form of polyploidy

thallus simple, flattened, nonleafy plant body

tilth soil structure characterized by open air spaces and high water storage capacity due to high levels of organic matter

tonoplast the membrane of the vacuole

topographic related to the shape or contours of the land

totipotent capable of forming entire plants from individual cells

toxin a poisonous substance

tracheid a type of xylem cell that conducts water from root to shoot

transcription factors proteins that bind to a specific DNA sequence called the promoter to regulate the expression of a nearby gene

translocate to move materials from one region to another

translucent allowing the passage of light

transmutation to change from one form to another

transpiration movement of water from soil to atmosphere through a plant

transverse across, or side to side

tribe a group of closely related genera

trophic related to feeding

turgor pressure the outward pressure exerted on the cell wall by the fluid within

twining twisting around while climbing

ultrastructural the level of structure visible with the electron microscope; very small details of structure

uniformitarian the geologic doctrine that formative processes on earth have proceeded at the same rate through time since earth's beginning

uplift raising up of rock layers, a geologic process caused by plate tectonics

urbanization increase in size or number of cities

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Used for storage and maintaining internal pressure

vascular plants plants with specialized transport cells; plants other than bryophytes

vascular related to the transport of nutrients, or related to blood vessels

vector a carrier, usually one that is not affected by the thing carried

vernal related to the spring season

vesicle a membrane-bound cell structure with specialized contents

viable able to live or to function

volatile easily released as a gas

volatilization the release of a gaseous substance

water table the level of water in the soil

whorl a ring

wort an old English term for plant; also an intermediate liquid in beer making

xenobiotics biomolecules from outside the plant, especially molecules that are potentially harmful

xeromorphic a form adapted for dry conditions

xerophytes plants adapted for growth in dry areas

zonation division into zones having different properties

zoospore a swimming spore

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

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Botanical and Scientific Illustrator
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College Professor
Curator of a Botanical Garden
Curator of an Herbarium
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plant sciences

plant sciences

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Preface

Someone once said that if you want to find an alien life form, just go into your backyard and grab the first green thing you see. Although plants evolved on Earth along with the rest of us, they really are about as different and strange and wonderful a group of creatures as one is likely to find anywhere in the universe.

The World of Plants

Consider for a minute just how different plants are. They have no mouths, no eyes or ears, no brain, no muscles. They stand still for their entire lives, planted in the soil like enormous drinking straws wicking gallon after gallon of water from the earth to the atmosphere. Plants live on little more than water, air, and sunshine and have mastered the trick of transmuting these simple things into almost everything they (and we) need. In this encyclopedia, readers will find out how plants accomplish this photosynthetic alchemy and learn about the extraordinary variety of form and function within the plant kingdom. In addition, readers will be able to trace their 450-million-year history and diversification, from the very first primitive land plants to the more than 250,000 species living today.

✶Explore further in Photosynthesis, Light Reactions and Evolution of Plants

All animals ultimately depend on photosynthesis for their food, and humans are no exception. Over the past ten thousand years, we have cultivated such an intimate relationship with a few species of grains that it is hardly an exaggeration to say, in the words of one scientist, that "humans domesticated wheat, and vice versa." With the help of agriculture, humans were transformed from a nomadic, hunting and gathering species numbering in the low millions, into the most dominant species on the planet, with a population that currently exceeds six billion. Agriculture has shaped human culture profoundly, and together the two have reshaped the planet. In this encyclopedia, readers can explore the history of agriculture, learn how it is practiced today, both conventionally and organically, and what the impact of it and other human activities has been on the land, the atmosphere, and the other creatures who share the planet with us.

✶Explore further in Agriculture, Modern and Human Impacts

Throughout history—even before the development of the modern scientific method—humans experimented with plants, finding the ones that provided the best meal, the strongest fiber, or the sweetest wine. Naming a thing is such a basic and powerful way of knowing it that all cultures have created some type of taxonomy for the plants they use. The scientific understanding of plants through experimentation, and the development of ra-

tional classification schemes based on evolution, has a rich history that is explored in detail in this encyclopedia. There are biographies of more than two dozen botanists who shaped our modern understanding, and essays on the history of physiology, ecology, taxonomy, and evolution. Across the spectrum of the botanical sciences, progress has accelerated in the last two decades, and a range of entries describe the still-changing understanding of evolutionary relationships, genetic control, and biodiversity.

✶Explore further in Ecology, History of; Biodiversity; and Phylogeny

With the development of our modern scientific society, a wide range of new careers has opened up for people interested in plant sciences, many of which are described in this encyclopedia. Most of these jobs require a college degree, and the better-paying ones often require advanced training. While all are centered around plants, they draw on skills that range from envisioning a landscape in one's imagination (landscape architect) to solving differential equations (an ecological modeler) to budgeting and personnel management (curator of a botanical garden).

✶Explore further in Curator of a Botanical Garden and Landscape Architect

Organization of the Material

Each of the 280 entries in *Plant Sciences* has been newly commissioned for this work. Our contributors are drawn from academic and research institutions, industry, and nonprofit organizations throughout North America. In many cases, the authors literally "wrote the book" on their subject, and all have brought their expertise to bear in writing authoritative, up-to-date entries that are nonetheless accessible to high school students. Almost every entry is illustrated and there are numerous photos, tables, boxes, and sidebars to enhance understanding. Unfamiliar terms are highlighted and defined in the margin. Most entries are followed by a list of related articles and a short reading list for readers seeking more information. Front and back matter include a geologic timescale, a topic outline that groups entries thematically, and a glossary. Each volume has its own index, and volume 4 contains a cumulative index covering the entire encyclopedia.

Acknowledgments and Thanks

I wish to thank the many people at Macmillan Reference USA and the Gale Group for their leadership in bringing this work to fruition, and their assiduous attention to the many details that make such a work possible. In particular, thanks to Hélène Potter, Brian Kinsey, Betz Des Chenes, and Diane Sawinski. The editorial board members—Robert Evans, Wendy Mechaber, and Robert Wallace—were outstanding, providing invaluable expertise and extraordinary hard work. Wendy is also my wife, and I wish to thank her for her support and encouragement throughout this project. My own love of plants began with three outstanding biology teachers, Marjorie Holland, James Howell, and Walt Tulecke, and I am in their debt. My many students at the Commonwealth School in Boston were also great teachers—their enthusiastic questions over the years deepened my own understanding and appreciation of the mysteries of the plant world. I hope that a new generation of students can discover some of the excitement and mystery of this world in *Plant Sciences.*

Richard Robinson
Editor in Chief

Geologic Timescale

Era	Period		Epoch	started (millions of years ago)
Cenozoic 66.4 millions of years ago–present time	**Quaternary**		Holocene	0.01
			Pleistocene	1.6
	Tertiary	**Neogene**	Pliocene	5.3
			Miocene	23.7
		Paleogene	Oligocene	36.6
			Eocene	57.8
			Paleocene	66.4
Mesozoic 245–66.4 millions of years ago	**Cretaceous**		Late	97.5
			Early	144
	Jurassic		Late	163
			Middle	187
			Early	208
	Triassic		Late	230
			Middle	240
			Early	245
Paleozoic 570–245 millions of years ago	**Permian**		Late	258
			Early	286
	Carboniferous	**Pennsylvanian**	Late	320
		Mississippian	Early	360
	Devonian		Late	374
			Middle	387
			Early	408
	Silurian		Late	421
			Early	438
	Ordovician		Late	458
			Middle	478
			Early	505
	Cambrian		Late	523
			Middle	540
			Early	570
Precambrian time 4500–570 millions of years ago				4500

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Hales, Stephen

English Physiologist
1677–1761

H

Stephen Hales was a preeminent scientist of the late eighteenth century and the founder of plant **physiology**. Born in Kent, England, in 1677, Hales grew up in an upper-class Kent family and was educated at Cambridge University. Though he received no formal training in botany during college, Hales obtained a solid background in science, including physics and mechanics. Upon graduation from Cambridge, Hales moved to Teddington, a town on the Thames River in England, where he lived the rest of his life.

physiology the biochemical processes carried out by an organism

Hales has been called the first fully **deductive** and **quantitative** plant scientist. He made many significant discoveries concerning both animal and plant circulation. Crucially, Hales measured plant growth and devised innovative methods for the analysis and interpretation of these measurements.

deductive reasoning from facts to conclusion

quantitative numerical, especially as derived from measurement

Hales's most original contribution was his transfer of application of the so-called statical method he and others had used on animals to plant **specimens**. The basis behind the statical method was the belief that the comprehension of living organisms was possible only through the precise measurements of their inputs and outputs. Thus the way to understand a human being would be to measure the fluids and other materials that had entered and left it. In the case of a tree, a statistician would measure changes in the amount and quality of the water it consumed and the sap it contained.

specimen object or organism under consideration

In 1706, under the influence of Isaac Newton's new mechanics, Hales tried to figure out the mechanism that controlled animal blood pressure by experimenting on dog specimens. At the same time, Hales had the idea that the circulation of sap in plants might well be similar to the circulation of the blood in humans and other animals. As he was exploring animal circulation, Hales grew increasingly interested in plant circulation. He wrote later in his book *Vegetable Staticks* of his first circulation experiments: "I wished I could have made the like experiments to discover the force of the sap in vegetables."

Stephen Hales.

After a decade of quiet research and study, Hales did indeed devise such experiments on plants. He attached glass tubes to the cut ends of vine plants. He then watched sap rise through these tubes, and he monitored how the sap flow varied with changing climate and light conditions. In 1724, Hales completed *Vegetable Staticks* (quoted above), wherein he distinguished three different aspects of water movement in plants. These he called imbibition, root pressure, and leaf suction.

The prevalent notion among Hales's contemporaries was that the movement of plant sap was similar to the circulation of human blood, which was discovered by William Harvey in 1628. Crucially, Hales demonstrated that this theory was false. Instead, he demonstrated the constant uptake (absorption) of water by plants and water's constant loss through transpiration (evaporation into the air). Drawing on this principle, Hales made many exact and careful experiments using weights and measures. All of these he repeated using different types of plants (willows and creepers, for example) in order to verify his conclusions. Thus, from his beginnings as a physiologist, Hales went on to create a mechanics of water movement. SEE ALSO DE SAUSSURE, NICHOLAS; PHYSIOLOGIST; PHYSIOLOGY, HISTORY OF; WATER MOVEMENT.

Hanna Rose Shell

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Halophytes

ions charged particles

ecosystem an ecological community together with its environment

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Use for storage and maintaining internal pressure

Halophytes (salt plants) are organisms that require elevated amounts of sodium up to or exceeding seawater strength (approximately 33 parts of sodium per thousand) for optimal growth. In contrast, most crops cease to produce with sodium at 1 to 3 ppt. Halophytes are found worldwide, including in deserts where infrequent rainfall leaches **ions** to the surface. They encroach into irrigated lands as ion concentrations increase over time. They are best known as mangroves, a term for a number of unrelated tree species, which in tropical **ecosystems** stabilize coastlines in species-rich habitats threatened by development. Halophytism characterizes species in many plant families, indicating adaptive evolution from nontolerant ancestors. Typical adaptations are succulence, water-conserving mechanisms, and specialized surface morphology (e.g., trichomes and waxes). Resistance to salinity is costly, explaining the slow growth of halophytes. Energy expenditure for ion pumping is required for sodium export (from glands), partitioning (movement of sodium away from growing tissues) or storage (in **vacuoles**, specialized cells, or senescing leaves). Another source of energy expenditure is for absorption of essential ions and nutrients from the soil. This active transport process is made more difficult by high levels of sodium in the surrounding soil. Valued for their ecological importance, few halophytes are economically significant, while species such as *Salicornia* have potential utility as oil crops. SEE ALSO COASTAL ECOSYSTEMS; DESERTS; TRICHOMES.

Hans Bohnert

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Red mangroves on a Florida coastline.

Herbals and Herbalists

For most of human history, people have relied on herbalism for at least some of their medicinal needs, and this remains true for more than half of the world's population in the twenty-first century. Much of our modern **pharmacopeia** also has its roots in the historical knowledge of medicinal plants.

pharmacopeia a group of medicines

What Are Herbs, Herbals, and Herbalists?

To botanists, herbs are plants that die back to the ground after flowering, but more generally, herbs are thought of as plants with medicinal, culinary (especially seasoning), or aromatic uses.

Traditional herbals are compilations of information about medicinal plants, typically including plant names, descriptions, and illustrations, and information on medicinal uses. Herbals have been written for thousands of years and form an important historical record and scientific resource. Many plant medicines listed in older herbals are still used in some form, but some herbals, especially earlier ones, also contain much inaccurate information and plant lore.

Herbalists follow a long tradition in using plants and plant-based medicines for healing purposes. Some gather medicinal plants locally, while others use both local and foreign plant material. Some rely on age-old knowledge and lore, while others also consult the findings of new research.

An engraving, circa 1713, showing various plants and corresponding body parts thought to benefit through some use of the plant.

Herbalism in History

There are herbalist traditions going back centuries or millennia in most parts of the world, and lists of medicinal plants survive from antiquity, such as Shen Nung's *Pen Ts'ao* (2800 B.C.E.) and the Egyptian *Papyrus Ebers* (1500 B.C.E.).

European herbal medicine is rooted in the works of classical writers such as Dioscorides, whose *De Materia Medica* (78 C.E.) formed the basis of herbals in Europe for 1,500 years. Then, as voyages of exploration began to bring new plants from faraway lands, European herbal authors expanded their coverage. This also led to a heightened interest in naming and classifying plants, contributing to the development of botanical science.

Significant European herbals include those by Otto Brunfels (c. 1488–1534), Leonhart Fuchs (1501–1566), Pier Andrea Mattioli (1500–1577), and John Gerard (1545–1612), among others. Reports from the New World include the Badianus manuscript (1552), an Aztec herbal by Martín de la Cruz and Juan Badiano, and works by Nicholas Monardes (1493–1588) and John Josselyn (fl. 1630–1675). Herbals were published in Europe into the eighteenth century but declined as modern medicine took new forms.

Herbal Medicine Today

Today, traditional herbalist healers continue to use knowledge passed down for generations. Some **ethnobotanists** are studying with traditional healers to save such knowledge before it disappears.

ethnobotanist a scientist who interacts with native peoples to learn more about the plants of a region

Due to a growing interest in alternative medicine, herbalism is also attracting new practitioners, and herbal research is constantly underway. Critics note that dosages can be difficult to control, even among plants of the same species, and side effects can be unpredictable.

A number of essential modern drugs derive from plants, and scientists generally agree that only a fraction of the world's plants have been studied for their medicinal potential. However, threats to the environment, particularly in tropical forests where the highest numbers of species (many still unknown to science) reside, may reduce the possibility of identifying new plant-derived drugs. SEE ALSO Ethnobotany; Herbs and Spices; Medicinal Plants; Taxonomy, History of.

Charlotte A. Tancin

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Herbaria

An herbarium is a collection of dried plants or fungi used for scientific study. Herbaria are the main source of data for the field of botany called taxonomy. Plant taxonomists study the **biodiversity** of a particular region of the world (**floristic** research) or the relationships among members of a particular group of organisms (monographic research). Although a plant looks different when it is dried compared to when it is growing in nature, most of the key features needed for taxonomic studies can be found in a well-

biodiversity degree of variety of life

floristic related to plants

LARGEST HERBARIA IN THE WORLD

Name	Location	Date Established	Number of Specimens (approximate)
Museum National d'Histoire Naturelle	Paris, France	1635	8,877,300
Royal Botanic Gardens	Kew, England	1841	6,000,000
New York Botanical Garden	New York, New York, U.S.A.	1891	6,000,000
Komarov Botanical Institute	St. Petersburg, Russia	1823	5,770,000
Swedish Museum of Natural History	Stockholm, Sweden	1739	5,600,000
The Natural History Museum	London, England	1753	5,300,000
Conservatoire et Jardin Botaniques	Geneva, Switzerland	1824	5,200,000
Harvard University	Cambridge, Massachusetts, U.S.A.	1864	5,000,000
Smithsonian Institution	Washington, D.C., U.S.A.	1848	4,858,000
Institut de Botanique	Montpellier, France	1845	4,368,000

SOURCE: Data from P. N. Holmgren, *Index Herbariorum,* 8th ed. (New York: New York Botanical Garden, 1990), Index.

specimen object or organism under consideration

prepared herbarium **specimen**. These features include the size and shape of the various parts of the organism, as well as surface texture, cellular structure, and color reactions with certain chemical solutions. From the investigation of these features, the taxonomist prepares a detailed description of the organism, which can be compared to descriptions of other organisms. Today it is possible to extract genetic material (deoxyribonucleic acid; DNA) from herbarium specimens. Gene sequences provide many data points for comparison between organisms.

Herbaria of the World

If prepared and maintained properly, herbarium specimens hold their scientific value for hundreds of years and therefore serve as a repository of information about Earth's current and past biodiversity. The oldest herbaria in the world, found in Europe, are more than three hundred years old. Traditionally all colleges or universities that offer training in plant science create and maintain herbaria, as do most botanical gardens and natural history museums.

There are approximately 2,639 herbaria in 147 countries around the world. Typically herbaria associated with smaller institutions concentrate on the plants and fungi of their regional flora, and perhaps additionally hold specimens representing the research interest of the faculty and graduate students. Larger herbaria strive to represent the plants and fungi from a wider geographic area and a greater diversity of organisms. Such herbaria may be housed in large natural history museums (the Field Museum of Natural History in Chicago, for example) or botanical gardens (such as the New York Botanical Garden), major research universities (such as Harvard University), or may be maintained by a governmental agency (such as the Smithsonian Institution).

When taxonomists publish a monograph or flora, they must provide a list of all the specimens examined in the course of the study, indicating the name of the herbarium where the specimens were deposited. Because the scientific method dictates that studies be replicable, anyone wanting to repeat a taxonomist's study has to begin by reexamining the specimens that were used.

OTHER U.S. HERBARIA

Major herbaria in the United States are the Missouri Botanical Garden in St. Louis, established in 1859 and holding 3.7 million specimens; the Field Museum of Natural History in Chicago, established in 1893 and holding 2.5 million specimens; and the University of California at Berkeley, established in 1872 and holding 1.7 million specimens.

Collecting and Preparing Specimens

Taxonomists not only examine specimens already deposited in herbaria, but also collect new herbarium specimens in the course of their research. When taxonomists go on collecting trips, they are equipped with tools such as plastic or waxed paper bags in which to place the individual specimens, clippers, knives, trowels, and perhaps a saw. Long poles with clippers attached to the ends or tree-climbing equipment may be used to collect flowers or leaves from tall trees. Collecting underwater plants such as algae may require hip boots, snorkel and face mask, or even scuba gear. Whatever the group of organisms, a good collection consists of just enough material to contain the important features for identification, such as leaves, roots, flowers, fruits, or other reproductive parts.

A collector always takes a field notebook on a collecting trip, because it is critical to record information about the organism as it is collected. The exact locality of a collected specimen is recorded using maps, compasses, or geo-positioning devices, which enables another collector to return to the same site if more material is needed. The collector also details the surroundings of the collected specimens, including the habitat (forest, meadow, or mountainside, for example), elevation, and what other types of plants or animals are found nearby. Also recorded are features that will change when the plant dries—such as its color, size, or odor—and a photograph of the organism or collection site may be taken.

It is necessary to remove as much of the moisture as possible from collected specimens to prevent decomposition by fungi or bacteria. For flowering plants, this is done by pressing the plant in absorbent paper and placing it between rigid boards (forming what's known as a plant press), and then placing the press over a source of heat. For fungi such as mushrooms, the specimen is instead placed whole (or sliced in half) on a drying apparatus that uses low heat and a fan to remove the water. Organisms such as lichens or mosses are air-dried for several days to remove moisture. Plants that contain a large amount of water are challenging to prepare as specimens. Cactus stems or large fruits such as pumpkins must be thinly sliced before pressing, and the absorbent material around the specimen must be replaced frequently.

When the specimen is dry, it is prepared for insertion in the herbarium. Preparing the specimen at this stage involves two steps: packaging and labeling. The typical pressed plant specimen is glued to a sheet of heavyweight paper, typically 27.5 x 43 centimeters in size. Specimens such as bryophytes, lichens, fungi, or very bulky plants are loosely placed in paper packets or boxes. Boxes are also used for specimens of very hard material such as coconut fruits or pine cones. Some plants and fungi are very tiny, consisting of a single cell, and therefore too small to see without a microscope. An herbarium specimen of such an organism is stored on a microscope slide. Whatever the size of the specimen, each is accompanied by a paper label, which includes the name of the plant and all of the information the collector recorded in his or her field book. In the past these labels were written by hand or manually typed. Today the collection data are more commonly entered into a computerized database and then formatted to print on a specimen label.

Preserving and Accessing Specimens

After an herbarium specimen is prepared, it is ready to be inserted in the herbarium. A modern herbarium holds its specimens in specially designed, air- and water-tight, sealed steel cases, which are divided internally into shelves or cubbyholes. When stored in such a case, herbarium specimens are protected from the greatest threats to their long-term maintenance, namely damage by water, insects, and fungi. Within an herbarium case, individual specimens are usually grouped by name or geographical region into folders or boxes.

An herbarium is usually maintained by a curator, a scientist responsible for overseeing the processing of new herbarium specimens, maintaining order within the collection, and guarding the specimens against damage. The curator is usually a taxonomist, chosen for the position because of his or her knowledge of the types of plants, fungi, or area that is the specialty of the herbarium. Large herbaria with important collections in many regions or groups of plants have many curators, each responsible for a particular part of the herbarium. In smaller university herbaria, the curator may also be a professor.

A curator is also responsible for overseeing the use of the herbarium by other scientists. Herbaria make their specimens available for study by visiting scientists and most also loan specimens to other herbaria when requested to do so. Herbarium curators want to make the specimens in their care available to all serious scientific studies. In addition to loaning specimens and welcoming other scientists into their herbaria, curators today often share searchable indices or catalogs, or even images of their collection through the World Wide Web. Scientists use the Internet for quick access to information about a specimen but generally still need to see the actual specimen to study it fully.

Although taxonomists are the most frequent users of herbaria, there are many other users. A forester might examine collections made over the years to see how biodiversity of the forest has changed over time. A conservation biologist might use an herbarium to see how the distribution of a rare or a weedy species has changed due to alterations in the environment. A government agency might use an herbarium to determine where to place roads or dams to cause the least disturbance to a biologically diverse area. A plant pathologist might use an herbarium to examine specimens that are the cause of plant diseases or to examine the distribution of the plant hosts of diseases to predict future areas of infection. Occasionally historians consult herbaria to learn more about the people who have collected plants over the years. For example, it is not well known that historical figures such as General George A. Custer, inventor George Washington Carver, or musician John Cage collected herbarium specimens, but collections made by all three have been found in the New York Botanical Garden herbarium, and other long-established herbaria probably contain equally surprising finds. SEE ALSO Curator of an Herbarium; Flora; Plant Identification; Systematics, Molecular; Systematics, Plant; Taxonomy.

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Herbicides

Herbicides are chemicals that kill plants. Herbicides are widely used in modern agriculture to control weeds, reduce competition, and increase productivity of crop plants. They are also used by homeowners to control lawn weeds and by turf grass managers, foresters, and other professionals. Herbicides are used not only on land, but also in lakes, rivers, and other aquatic environments to control aquatic weeds.

The modern use of herbicides began in the 1940s, with the development of 2,4-D (2, 4-dichlorophenelyacetic acid). By the end of that decade, herbicide use had grown from a few thousand acres to several million. There are now approximately four hundred different herbicides registered for use in the United States. While the rates of application vary by crop, the vast majority of commercial agricultural crop acreage receives at least one application of herbicide every year.

Herbicides may be applied directly to the soil or to the leaves of the target plant. Soil applications may be targeted at preventing seed germination, to affect root growth, or to be absorbed and to work systemically (within the whole plant body). Foliar (leaf) applications may target the leaves or be absorbed. In addition to directly killing the target weed, herbicides can, over time, reduce the number of weed seeds in the soil, decreasing the need for continued intensive applications in the future.

A row of Worcester Pearmain apple trees in an English orchard. Seven weeks after the trees were treated with an herbicide, the grass beneath turned brown and died.

auxin a plant hormone

compound a substance formed from two or more elements

Herbicides kill plants by interfering with a fundamental process within their cells. 2,4-D is a synthetic **auxin**. It promotes cell elongation (rather than cell division), and in effective concentrations kills the target plant by causing unregulated growth. Plants treated with 2,4-D display misshapen stems, inappropriate adventitious root growth, and other aberrant effects (growing in an unusual location on the plant). The excessive growth exhausts food reserves, and the combination of effects eventually causes the death of the plant. 2,4-D is often used to kill dicot weeds growing among monocot crops, since monocots are more resistant to its effects. 2,4-D and a related **compound**, 2,4,5-T were combined in Agent Orange, the defoliant used in the Vietnam War. Health effects from exposure to Agent Orange are believed to be due to contamination with dioxin, and not to the herbicides themselves.

Glyphosphate (marketed as Roundup®) interferes with an enzyme involved in amino acid synthesis, thereby disrupting plant metabolism in a variety of ways. It is one of the most common herbicides and is available for homeowner use as well as for commercial operators. Glyphosphate is a nonselective herbicide, killing most plants that it contacts. However, it is fairly harmless to animals, including humans, since amino acid metabolism is very different in animals. A gene for glyphosphate resistance has now been introduced into a number of important crop plants, allowing increased use of glyphosphate to control weeds on these crops.

chloroplast the photosynthetic organelle of plants and algae

reaction center a protein complex that uses light energy to create a stable charge separation by transferring a single electron energetically uphill from a donor molecule to an acceptor molecule, both of which are located in the reaction center

free radicals toxic molecular fragments

Atrazine interferes with photosynthesis. Atrazine is taken up by roots and transported to **chloroplasts**, where it binds to a protein in the Photosystem II **reaction center**. This prevents the normal flow of electrons during photosynthesis and causes chloroplast swelling and rupture.

Paraquat also interferes with photosynthesis, but through a different mechanism. This herbicide accepts electrons from photosystem I and then donates them to molecular oxygen. This forms highly reactive oxygen **free radicals**, which are immediately toxic to the surrounding tissue. Paraquat is also toxic to humans and other animals.

As with any agent that causes death in a group of organisms, herbicides cause natural selection among weed species. Evolution of herbicide resistance is a serious problem and has spurred research on new herbicide development and a deeper understanding of mechanisms of action. These concerns have joined with environmental and health concerns to promote a more integrated approach to weed management, combining tillage practices, selection for weed-tolerant varieties, better understanding of weed biology, and better timing of herbicide application. This integrated approach requires more time and attention from the farmer but can also offer significant benefits. SEE ALSO Agriculture, Modern; Dicots; Hormones; Monocots; Photosynthesis, Light Reactions and.

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Herbs and Spices

The terms *herb* and *spice* are popular terms for plants or plant products that are used as flavorings or scents (e.g., spices and culinary herbs), drugs (e.g., medicinal herbs), and less frequently as perfumes, dyes, and stimulants.

Many herbs and spices are edible but may be distinguished from fruits and vegetables by their lack of food value, as measured in calories. Unlike fruits and vegetables, their usefulness has less to do with their primary metabolites (e.g., sugars and proteins) than with their secondary metabolites (**compounds** commonly produced to discourage **pathogens** and predators). The distinct flavors and smells of spices and culinary herbs are usually due to essential oils, while the active components of medicinal herbs also include many kinds of steroids, alkaloids, and glycosides. Most plants referred to as herbs or spices contain many different secondary compounds.

The bark of cinnamon, a commercially important spice.

compound a substance formed from two or more elements

pathogen disease-causing organism

exudation releasing of a liquid substance; oozing

Spices

Spices are pungent, aromatic plant products used for flavoring or scent. The derivation of the word spice from the Latin *species*, meaning articles of commerce, suggests that these were plants that early Europeans could not grow, but instead had to trade for via Asia or Africa. Consistent with this, people tend to limit the word spice to durable products such as seeds, bark, and resinous **exudations**, especially those from subtropical and tropical climates, and use the word herb when the useful part is the perishable leaf. Commercially important spices include black pepper, the fruit of *Piper nigrum*, and cinnamon, the inner bark of two closely related tree species from the laurel family.

Culinary Herbs

The word herb is popularly used to refer to a plant product that has culinary value as a flavoring, while scientifically an herb is a plant that lacks permanent woody stems. Most of our well-known culinary herbs are obtained from the leaves or seeds of herbaceous plants, many of which originated in the Mediterranean region of Europe. Many of the best known belong to the mint family, such as peppermint (*Mentha* x *piperita*), or the carrot family, such as coriander (*Coriandrum sativum*).

Herbal Medicines

pharmacopeia a group of medicines

Medicinal herbs were once the mainstays of all medicine and include plants that range from edible to extremely toxic. Every culture has developed its own herbal **pharmacopeia,** with herbs taken as teas or tinctures, smoked, or applied to the body as poultices or powders. While much of the world still depends on herbal-based medicine, western medical practitioners rely mainly on synthetic drugs. Some of these are synthetic copies of the active compounds found in older herbal remedies, while others are more effective chemicals modeled on these naturally occurring compounds. At least thirty herbal drugs still remain important in western medicine. Some are obtained directly from plants, such as digitoxin from the woolly foxglove (*Digitalis lanata*), which is used to treat congestive heart failure, while others are the result of refinement and manipulation of plant products, including oral contraceptives from yams (*Dioscorea* species). Recent years have seen some resurgence in the use of traditional herbal medicines in many western cultures. SEE ALSO Alkaloids; Cultivar; Dioscorea; Economic Importance of Plants; Flavor and Fragrance Chemist; Herbals and Herbalists; Medicinal Plants; Oils, Plant-Derived; Tea.

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History of Plant Sciences

See Ecology, History of; Evolution of Plants, History of; Physiology, History of; Taxonomy, History of.

Hooker, Joseph Dalton

British Botanist
1817–1911

Joseph Dalton Hooker.

Joseph Dalton Hooker was one of the leading British botanists of the late nineteenth century. He was born in Halesworth, Sussex, and was the son of another great British botanist, Sir William Jackson Hooker (1785–1865). Hooker graduated with a degree in medicine from Glasgow University, where his father was a professor of botany. His father eventually held the position of Director of Kew Gardens in London and, through his leadership, made it one of the finest botanical gardens in the world, with an extensive collection of plants from the British colonies. In 1855 Joseph Hooker became assistant director of Kew Garden and became director when his father died in 1865.

Hooker is best known for his work in taxonomy, the science of classification, and plant geography, the science of plant distribution. These primary interests were shaped by his participation in a famous four-year scientific expedition under the command of Captain James Clark Ross that sought to determine the position of the south magnetic pole. Hooker was aboard the H.M.S. *Erebus*, one of the two expeditionary ships that left England in 1839. Although he was appointed the ship's assistant surgeon, Hooker made extensive collections of botanical material from geographic regions not previously explored, including the Great Ice Barrier and several oceanic islands such as Tasmania, the Falklands, and New Zealand. Hooker was struck by the similarity of the floras of these regions. He explained these similarities by adopting a land-bridge theory, one that postulated the existence of a lost circumpolar continent. It was on the basis of these observations that Hooker began to adopt an evolutionary explanation for the similarities. His work was summarized in a collection known as *The Botany of the Antarctic Voyage of H.M. Discovery Ships Erebus and Terror.* The publication of its six quarto volumes between 1853 and 1855 established Hooker as one of the great botanists of the nineteenth century.

Hooker continued to travel and explore through much of his life, and in the process compiled many floras. He also collected many plant specimens, which he introduced to England. He is especially well known for his stunning, previously unknown species of *Rhododendron* that he discovered in the Sikkim region of the Himalayas. Many of these are still grown in Kew Gardens. He also made notable contributions in pure morphology, including classic studies on the unusual plant *Welwitschia* (1863).

Hooker is also known for his close friendship with the most famous naturalist of his day, Charles Darwin (1809–1882). In fact, Darwin trusted Hooker enough to confide his radical new theory of descent with modification by means of natural selection (later called evolution by means of natural selection) in 1844, some fifteen years before Darwin wrote *On the Origin of Species* (1859). Although Hooker knew of this theory well in advance of its publication, he was not convinced of its importance until his own observations of the distribution of plants were completed. Darwin and Hooker remained close friends until Darwin's death. Hooker led a long and productive life and was knighted in 1877. He died in Sunningdale, England, in 1911. SEE ALSO BIOGEOGRAPHY; BOTANICAL GARDENS AND ARBORETA; CURATOR OF A BOTANICAL GARDEN; DARWIN, CHARLES; TAXONOMIST; TAXONOMY.

Vassiliki Betty Smocovitis

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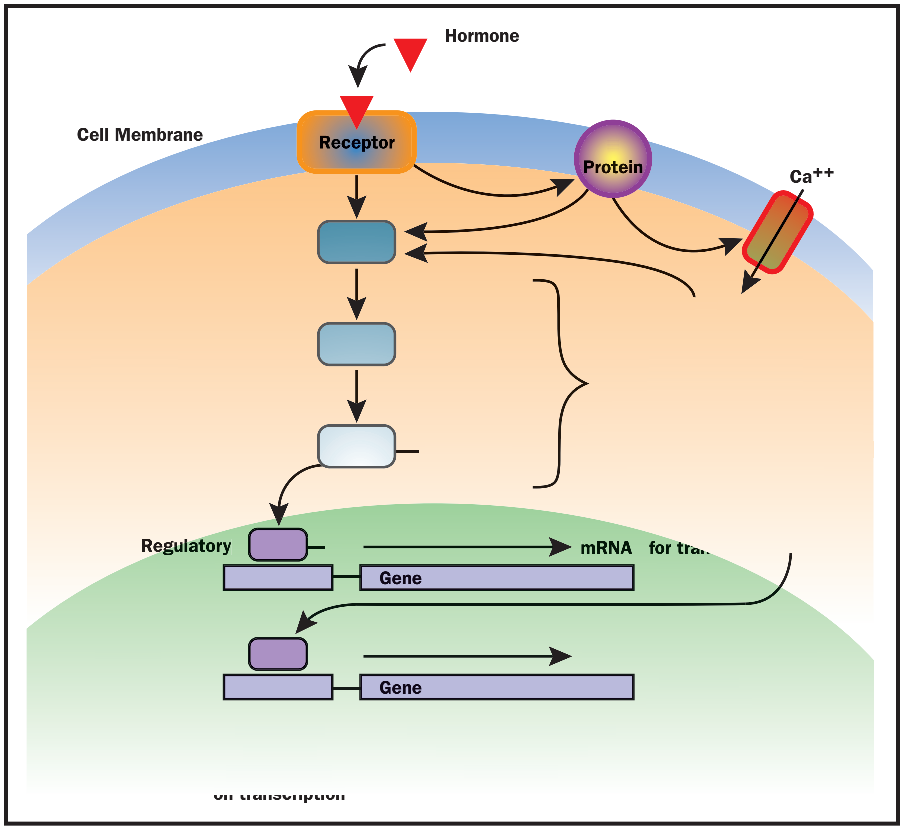
Hormonal Control and Development

Plant hormones are a group of naturally occurring organic substances that, at low concentrations, influence physiological processes such as growth, differentiation, and development. Many plant hormones are transported from one place in the plant to another, thus coordinating growth throughout the plant, while others act in the tissues in which they are produced.

For a hormone to have an effect it must be synthesized, reach the site of action, be detected, and have that detection transferred into a final biochemical action. The steps following detection are called signal transduction, while the components of the signal transduction chain are referred to as second messengers. Because the concentration of hormone molecules affects the intensity of the response, the level of the hormone is also significant. The level is determined by the **biosynthesis** of the active hormone molecule and its removal by metabolism to inactive byproducts, or its binding to molecules like sugars, which also has an inactivating effect. Plant scientists have investigated these phenomena by analyzing the levels and biochemical forms of the hormones present in relation to differences in development. Recently the use of mutants and bioengineered plants in which growth or development is abnormal has enabled us to start understanding how hormones work. This research has been coupled with the isolation of the genes and proteins that are needed for the normal functioning of the hormone.

biosynthesis creation through biological pathways



Generalized signal transduction scheme, which may or may not proceed via a membrane G-protein and/or the production of a protein gene regulator (transcription factor). The final effect is the activation of transcription of a gene producing one or more proteins that brings about the effect on growth or development.

auxin a plant hormone

precursor a substance from which another is made

carotenoid a colored molecule made by plants

vascular related to transport of nutrients

Biosynthesis. **Auxin** (indoleacetic acid, IAA) is synthesized from indoleglycerophosphate, the **precursor** to the amino acid tryptophan, and, in some plants, from tryptophan itself. GA_1, the principal active gibberellin in most plants, is synthesized via the isoprenoid pathway, followed by a series of many other gibberellin intermediates. The level of GA_1 is very tightly regulated. The genes for the enzymatic conversions have been isolated, and the transcription of these genes have been shown to be under both feedback and environmental control. Gregor Mendel's tallness gene encodes a step in the gibberellin biosynthesis pathway just before GA_1. Cytokinins are synthesized by the attachment of an isopentenyl side chain to adenosine phosphate. The enzyme for this process, isopentenyl transferase, is the main regulating step in cytokinin biosynthesis, and its gene has been used in the genetic transformation of plants to enhance cytokinin levels. Abscisic acid is synthesized via **carotenoid** molecules. Ethylene is derived from methionine via the nonprotein amino acid ACC (1-amino-cyclopropane-1-carboxylic acid). The transcription of the genes for the enzymes making ACC and its conversion into ethylene is under precise developmental control, notably during fruit ripening.

Transport. Most hormones simply travel along with the contents of the xylem or phloem by a combination of diffusion and bulk transport. Auxin is special in that it is transported primarily in the cells of the **vascular** cambium or its initials and is moved away from the tip of the stem or root where it is synthesized (termed *polar transport*). Auxin enters the cell from the cell wall above as an un-ionized molecule (because the wall has an acidic pH) that can cross the cell membrane. At the neutral pH inside the cell it becomes ionized, preventing its outward diffusion through the cell membrane. Outward transport is on special carrier proteins located only at the base of the cell, so movement is downward. (In roots, the situation is reversed.) When a stem is placed on its side the carriers most likely migrate to the side of the lower cell so that the auxin is transported to the lower side of the stem, causing increased growth on that side and a bending upwards. This is thought to account at least in part for gravitropism, or growth away from the ground. The genes for the transport proteins have been isolated.

Detection. For a hormone molecule to have an effect it must bind to a receptor protein. *Arabidopsis* mutants that do not respond to ethylene have been used to study the ethylene receptor. It is located in the cell membrane with parts that react with the next signaling compound exposed on the inside of the cell. Copper has been shown to coordinate the binding of ethylene to the receptor site. The auxin binding protein is located in the **endoplasmic reticulum**, from which it also migrates to the cell membrane. Its gene has also been isolated.

endoplasmic reticulum membrane network inside a cell

Signal Transduction. Following detection, the signal from the presence of the hormone molecule has to be translated into action. There are usually many steps in this process, although a general pattern can be seen. Often the hormone triggers the phosphorylation of an activator protein, which then binds to the regulatory region of a gene, thus turning on gene transcription. This gene may produce the final product, or may itself produce a gene regulator (or **transcription factor**). Steps prior to the phosphorylation of the regulatory protein may include an interaction with a membrane G protein that in turn releases other factors and the opening of calcium channels in the membrane permitting an increase in the cytoplasmic level of calcium. Some aspects of action appear, however, to be more direct, not needing gene transcription per se, although some signal transduction is always involved. The mode of action varies from hormone to hormone, and even between different hormone actions, as described below.

transcription factors proteins that bind to a specific DNA sequence called the promoter to regulate the expression of a nearby gene

Auxin in Cell Elongation. Cell elongation is a vital part of growth. Auxin causes cell elongation within ten minutes by making the cell walls more extensible. This occurs through a series of steps: Auxin stimulates the pumping of hydrogen **ions** out of the protoplast via proton pumps driven by adenosine triphosphate (**ATP**), so acidifying the wall; this activates an enzyme called expansin, which is activated by acid conditions (about pH 4.5); expansin breaks the hydrogen bonds between the cellulose **microfibrils** of the wall and the other sugar-chain molecules that cross-link the microfibrils; the cell walls are made more extensible; and the cell then elongates because of the **turgor pressure** inside the cell.

ions charged particles

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

microfibrils microscopic fibers

turgor pressure the outward pressure exerted on the cell wall by the fluid within

Auxin also has a rapid action on promoting the transcription of a number of auxin-specific genes, whose exact function is currently unknown. It is uncertain whether auxin activates preexisting proton pumps in the cell membrane or whether it induces synthesis of new proton pumps. Auxin also stimulates the transcription of genes for other enzymes that act on other cell wall polymers.

Gibberellin in Alpha-Amylase Production in Cereal Grains. Germinating seeds need to mobilize their stored carbohydrates to grow. In germinating cereal grains, gibberellin promotes the synthesis of the enzyme alpha-

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

amylase in cells of the aleurone surrounding the **endosperm**. The alpha-amylase breaks down the starch of the endosperm into sugars for transport to the growing seedling. Gibberellin acts through second messengers to promote transcription of the gene for alpha-amylase. Gibberellin first binds at the surface of the aleurone cell. The initial steps in the transduction chain are unknown, but gibberellin rapidly promotes the biosynthesis of a transcription-promoting factor named GA-myb. GA-myb binds to specific regulatory regions of the alpha-amylase gene, so turning on the transcription of the alpha-amylase mRNA, which is translated to produce alpha-amylase.

Gibberellin in Stem Elongation. The presence of gibberellin is normally needed for stems to elongate, and gibberellin-deficient mutants are usually dwarf. This has been explained by the idea that a protein factor in the signal transduction chain has the effect of preventing growth, but in the presence of gibberellin this factor is negated, allowing growth to proceed. However, a further mutation of a dwarf *Arabidopsis* has produced a tall plant, even though the level of gibberellin is still deficient. In the double mutant the inhibitory protein factor is negated because of a mutation in its structure, allowing growth to proceed. There is also genetic evidence of a second negative regulator in the signal transduction chain. At the present time we do not know the end product that actually promotes or inhibits the elongation of the cell.

solute a substance dissolved in a solution

Abscisic Acid (ABA) and Stomatal Closure. Stomata are leaf surface pores surrounded by guard cells. ABA promotes stomatal closure by causing the exit of potassium ions from the guard cells. K^+ is the main **solute** causing turgor in the guard cells and opening the stoma. ABA binds to a cell-surface receptor on the surface of the guard cells. This causes a calcium ion influx and an increase in the level of inositol triphosphate, a signaling molecule, which causes a release of calcium from internal stores. The Ca^{++} brings about a membrane depolarization, triggering the outward K^+ ion channels to open. Calcium also has a direct effect on the potassium ion channels via the phosphorylation of a specific protein in guard cell protoplasts.

Ethylene and Seedling Stem Growth. Exposure of *Arabidopsis* seedlings to ethylene usually causes stunted growth. However, some mutants are insensitive to ethylene. Other mutants grow stunted, as if they were exposed to ethylene, even when they are not. These mutants have helped the investigation of ethylene signal transduction. Ethylene's receptor interacts with a protein that blocks an ion channel. In the presence of ethylene, the receptor causes the protein to unblock the channel. The entry of (unknown) ions then activates other second messengers. Activation results in the synthesis of a transcription factor, finally triggering the synthesis of specific enzymes that can cause stunted growth. In ripening fruit, ethylene promotes the transcription of the mRNAs that encode for many enzymes that produce the chemical changes, including color, taste, and softening, which we know as ripening. This presumably occurs via a similar transduction chain, but the paucity of mutants makes it more difficult to investigate than in *Arabidopsis*. SEE ALSO Genetic Mechanisms and Development; Hormones.

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Hormones

Hormones are small molecules that are released by one part of a plant to influence another part. The principal plant growth hormones are the auxins, gibberellins, cytokinins, abscisic acid, and ethylene. Plants use these hormones to cause cells to elongate, divide, become specialized, and separate from each other, and help coordinate the development of the entire plant. Not only are the plant hormones small in molecular weight, they are also active in the plant in very small amounts, a fact that made their isolation and identification difficult.

The first plant growth hormones discovered were the auxins. (The term *auxin* is derived from a Greek word meaning "to grow.") The best known and most widely distributed hormone in this class is indole-3-acetic acid. Fritz W. Went, whose pioneering and ingenious research in 1928 opened the field of plant hormones, reported that auxins were involved in the control of the growth movements that orient shoots toward the light, and that they had the additional, striking quality of moving only from the shoot tip toward the shoot base. This polarity of auxin movement was an inherent property of the plant tissue, only slightly influenced by gravity. Other less-investigated auxins include phenyl-acetic acid and indole-butyric acid, the latter long used as a synthetic auxin but found to exist in plants only in 1985.

The gibberellins are a family of more than seventy related chemicals, some active as growth hormones and many inactive. They are designated by number (e.g., GA_1 and GAL_{20}). GA_3 (also called gibberellic acid) is one of the most active gibberellins when added to plants. Slight modifications in the basic structure are associated with an increase, decrease, or cessation of biological activity: each such modified chemical is considered a different gibberellin.

Cytokinins are a class of chemical **compounds** derived from adenine that cause cells to divide when an auxin is also present. Of the cytokinins found in plants, zeatin is one of the most active.

compound a substance formed from two or more elements

Abscisic acid helps protect the plant from too much loss of water by closing the small holes (stomata) in the surfaces of leaves when wilting begins.

PLANT HORMONES AND THEIR FUNCTIONS

Hormone	Functions
Auxins (indoleacetic acid; IAA)	Stimulates shoot and root growth; involved in tropisms; prevents abscission; controls differentiation of xylem cells and, with other hormones, controls sieve-tube cells and fibers
Gibberellins	Stimulates stem elongation, seed germination, and enzyme production in seeds
Cytokinins	Stimulates bud development; delays senescence; increases cell division
Abscisic acid	Speeds abscission; counters leaf wilting by closing stomates; prevents premature germination of seeds; decreases IAA movement
Ethylene (gas)	Produced in response to stresses and by many ripening fruits; speeds seed germination and the ripening of fruit, senescence, and abscission; decreases IAA movement

The only known gas that functions as a plant growth hormone is the small C_2H_2 molecule called ethylene. Various stresses, such as wounding or waterlogging, lead to ethylene production.

Major Effects of the Principal Plant Growth Hormones

Auxins. Indoleacetic acid (IAA), produced primarily in seeds and young leaves, moves out of the leaf stalk and down the stem, controlling various aspects of development on the way. IAA stimulates growth both in leaf stalks and in stems. In moving down the leaf stalk, IAA prevents the cells at the base of the leaf from separating from each other and thus causing the leaf to drop (called leaf abscission). The speed of IAA polar movement through shoot tissues ranges from 5 to 20 millimeters per hour, faster than speeds for the other major hormones.

The growth responses of plants to directional stimuli from the environment are called tropisms. Gravitropism (also called geotropism) refers to a growth response toward or away from gravity. Phototropism is the growth response toward or away from light. These tropisms are of obvious value to plants in facilitating the downward growth of roots into the soil (by positive gravitropism) and the upward growth of shoots into the light (by positive phototropism, aided by negative gravitropism).

lateral away from the center

The role of auxin in controlling tropisms was suggested by Went and N. Cholodny in 1928. Their theory was that auxin moves laterally in the shoot or root under the influence of gravity or one-sided light. Greater concentration on one side causes either greater growth (in the case of the shoot) or inhibited growth (in roots). This Cholodny-Went theory of tropisms has been subject to refinement and question for decades. Evidence exists, for instance, that in some plants tropism toward one-sided light results not from **lateral** movement of auxin to the shaded side, but rather from production of a growth inhibitor on the illuminated side.

apical at the tip

A widespread, though not universal, effect of IAA moving down from the young leaves of the **apical** bud is the suppression of the outgrowth of the side buds on the stem. This type of developmental control is called apical dominance: if the apical bud is cut off, the side buds start to grow out (released from apical dominance). If IAA is applied to the cut stem, the side buds remain suppressed in many plants.

vascular related to transport of nutrients

In addition to enhancing organ growth, IAA also plays a major part in cell differentiation, controlling the formation of xylem cells and being involved in phloem differentiation. In its progress down the stem, IAA stimulates the development of the two main **vascular** channels for the movement of substances within the plant: xylem, through which water, mineral salts, and other hormones move from the roots; and phloem, through which various organic compounds such as sugars move from the leaves. In plants that develop a cambium (the layer of dividing cells whose activity allows trees to increase in girth), the polarly moving IAA stimulates the division of the cambial cells. Cut-off pieces of stem or root usually initiate new roots near their bases. As a result of its polar movement, IAA accumulates at the base of such excised pieces and touches off such root regeneration. In the intact plant, the shoot-tip toward shoot-base polar movement of IAA continues on into the root, where IAA moves toward the root tip primarily in the stele (the inner column of cells in the root).

Interesting effects of IAA have been found in a more limited number of plant species. Plants of the Bromeliad family, which includes pineapples, start to flower if treated with IAA. Some other plants typically produce flowers that can develop as either solely male or solely female flowers depending on various environmental factors: In several such species IAA stimulates femaleness.

Gibberellins (GAs). Produced in young leaves, developing seeds, and probably in root tips, the biologically active GAs, such as GA_1 and GA_3, move in shoots without polarity and at a slower rate than IAA down the stems where they cause elongation. In roots they show root-tip toward root-base polar movement—the opposite of IAA. Their effect on stem elongation is particularly striking in some plants that require exposure to long days in order to flower. In such plants the stem elongation that precedes flowering is caused by either long days or active GAs and is so fast that it is called bolting. A similar association of light effects and active GAs is found in seeds that normally require light or cold treatment to germinate. GAs can substitute for these environmental treatments. In cereal seeds, GA, produced by the embryos, moves into the parts of the seeds containing starch and other storage products. There the GA triggers the production of various specific **enzymes** such as alpha-amylase, which breaks down starch into smaller compounds usable by the growing embryos. In the flowers that can develop as either male or female, active GAs cause maleness (the opposite effect to that of auxin). Not surprisingly, in view of the relatively large amounts of GAs in seeds, spraying GAs on such seedless grape varieties as Thompson produces bigger and more elongated grapes on the vines.

enzyme a protein that controls a reaction in a cell

Cytokinins. Produced in roots and seeds, the cytokinins' often-reported presence in leaves apparently results from accumulation of cytokinins produced by roots and moved to the shoot through the xylem cells. Research using pieces of plant tissue growing in test tubes revealed that adding cytokinins increased cell divisions and subsequently the number of shoot buds that regenerated, while increasing the amount of added IAA increased the number of roots formed. The test-tube cultures could be pushed toward bud or root formation by changing the ratio of cytokinin to IAA. The growth of already-formed lateral buds on stems could be stimulated in some plants by treating the lateral buds directly with cytokinins. With IAA from the apex of the main shoot inhibiting outgrowth of the lateral buds and with cytokinins stimulating their outgrowth, the effects of the two hormones on lateral buds suggests a balancing effect like that seen in root/shoot regeneration in the tissue cultures. Treatment with cytokinins retards the senescence of leaves, and naturally occurring leaf senescence is accompanied by a decrease in native cytokinins. When the movement of cytokinins such as zeatin through excised **petioles** was tested in the same sort of experiment that showed IAA moving with polarity at 5 to 10 millimeters per hour, cytokinins showed the slower rate of movement and the lack of polarity characteristic of GAs. However, through root sections, zeatin movement was **nonpolar**, unlike the movement of GAs.

petiole the stalk of a leaf, by which it attaches to the stem

nonpolar not directed along the root-shoot axis

Abscisic Acid. Abscisic acid is found in leaves, roots, fruits, and seeds. In leaves that are not wilting, the hormone is mostly in the **chloroplasts**. When wilting starts the abscisic acid is released for movement to the guard cells

chloroplast the photosynthetic organelle of plants and algae

of the stomates. Abscisic acid moves without polarity through stem sections and at the slower rate typical of GAs and cytokinins.

abscission the separation of a leaf or fruit from a stem

As its name implies, abscisic acid stimulates leaf or fruit **abscission** in many species, as evidenced by faster abscission from treating with the hormone and by increases in the amount of native abscisic acid in cotton fruits just prior to their natural abscission. Abscisic acid's most investigated effect, however, is its protection of plants from too much water loss (wilting) by closing the stomates in leaves when wilting starts. The onset of wilting is accompanied by fast increases in the abscisic acid levels in the leaves and subsequent closure of the stomates. Spraying the leaves with abscisic acid causes stomate closure even if the leaves are not wilting. In seeds, abscisic acid prevents premature germination of the seed.

Ethylene Gas. Ethylene gas is produced by many parts of plants when they are stressed. Also, normally ripening fruits are often rich producers of ethylene. Among ethylene's many effects are speeding the ripening of fruits and the senescence and abscission of leaves and flower parts; indeed, it is used commercially to coordinate ripening of crops to make harvesting more efficient. Ethylene gas releases seeds from dormancy. If given as a pretreatment, it inhibits the polar movement of auxin in stems of land plants (but, surprisingly, increases auxin movement in some plants that normally grow in fresh water). Ethylene moves readily through and out of the plant. The stimulation of flowering in pineapple and other bromeliads by spraying with IAA, mentioned earlier, is due to ethylene produced by the doses of auxin applied. Despite its frequent production by plants, ethylene is apparently not essential for plant development. Mutations or chemicals that block ethylene production do not prevent normal development.

Interactions of Hormones

In addition to the many effects on development of individual plant growth hormones, a sizeable number of effects of one hormone on another have been found. For example, IAA alone can restore the full number of normal tracheary cells in the xylem, but to restore the full number of sieve-tube cells in the phloem zeatin is needed in addition to IAA. Similarly, to restore the full number of fibers in the phloem, GA must be added along with IAA.

basipetal toward the base

Hormones affect each other's movement, too. Mentioned above was the decrease in IAA movement from pretreatment with ethylene. Similarly, abscisic acid decreases the **basipetal** polar movement of IAA in stems and petioles. Therefore, in view of IAA's role as the primary inhibitor of abscission in plants, the abscisic acid-induced decrease in IAA movement down the leaf stalk toward the abscision zone probably explains at least part of abscisic acid's role as an accelerator of abscission. In other cases, increases in IAA basipetal movement have resulted from GA or cytokinin treatment. The nonpolar movement typical of cytokinins was changed to polar movement when IAA was added, too. SEE ALSO Differentiation and Development; Embryogenesis; Genetic Mechanisms and Development; Germination and Growth; Hormonal Growth and Development; Photoperiodism; Seedless Vascular Plants; Senescence; Tropisms.

William P. Jacobs

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Horticulture

The word *horticulture* translates as "garden cultivation," or to cultivate garden plants. It was first used in publication in 1631 and was an entry in *The New World of English Words* in 1678. Today horticulture means the science, technology, art, business, and hobby of producing and managing fruits, vegetables, flowers and ornamental plants, landscapes, interior plantscapes, and grasses and turfgrasses. Although horticulture has been practiced for several millennia, it became a recognized academic and scientific discipline as it emerged from botany and medicinal botany in the late nineteenth century. Liberty Hyde Bailey, professor of horticulture at both Michigan State and Cornell Universities, is credited as the father of American horticulture, as he founded the first academic departments of horticulture.

Modern horticulture encompasses plant production (both commercial and gardening) and science, both practical and applied. Horticulture and the associated green industries are a rapidly developing professional field with increasing importance to society. The direct "farm-gate" value of horticultural crop production in the United States exceeds $40 billion; the overall value to the economy is much higher due to value added in preparation and preservation, or installation, and use and maintenance of horticultural plants and products.

Horticultural plants include fresh fruits and vegetables, herbaceous annual and perennial flowering plants, flowers produced as cut flowers for vase display, woody shrubs and trees, ornamental grasses, and turfgrasses used for landscapes and sports facilities. The crops encompass plants from tropical areas (fruits, vegetables, and tropical foliage plants) to those from the temperate zone. Horticulture crops are typically consumed or used as freshly harvested products and therefore are short-lived after harvest. Product quality, nutrition, flavor, and aesthetic appearance are important attributes of horticultural crops and are the goal of production and management. The production of horticultural plants is typified by intense management, high management cost, environmental control, significant technology use, and high risk. However, the plants, because of their high value as crops, result in very high economic returns. Horticultural crop plant production and maintenance requires extensive use of soil manipulation (including use of artificial or synthetic soil mixes), irrigation, fertilization, plant growth regulation, pruning/pinching/trimming, and environmental control. Plants can be grown in natural environments, such as orchards, vineyards, or groves for fruits, grapes, nuts, and citrus, or as row crops for vegetables. Plants can also be produced in very confined environments, such as in nurseries, greenhouses, growth rooms, or in pots. Horticultural plants exhibit wide variation and diversity in their cultivated varieties (cultivars) with differences in flower or fruit color and plant shape, form, size, color, or flavor and aroma adding to that diversity and to the plants' value.

Horticultural plants are very important to human health and well being and are critical to the environment of homes, communities, and the world. Horticulture food crops play an important role in human nutrition. The U.S. Department of Agriculture (USDA) recommends five to nine servings of fruits and vegetables be consumed daily to provide important nutrients and vitamins and to maintain overall good health. The use of landscape plants has been demonstrated to increase the property value of homes and improve communities and the attitudes of those owning or using the property. Use of plants in the landscape, development of public parks and greenbelts, and planting trees all help remediate pollution and contribute to production of oxygen in the air. Plants used indoors, whether flowers or house plants or interior plant scaping, improve the indoor environment by purifying air, removing some pollutants and dusts, and adding beauty, thereby improving the attitude and well being of those who occupy or use the inside areas.

hybridization formation of a new individual from parents of different species or varieties

A number of techniques are used in horticulture. New plant cultivars are developed through plant **hybridization** and genetic engineering. The number of plants is increased through plant propagation by seeds, cuttings, grafting, and plant tissue and cell culture. Plant growth can be controlled by pinching, pruning, bending, and training. Plant growth, flowering, and fruiting can also be controlled or modified by light and temperature variation. Further, growth and flowering can be altered by the use of growth-regulating chemicals and/or plant hormones. The rate of plant growth and quality of plant products are controlled by managing fertilizer and nutrient application through **fertigation** or **hydroponic** solution culture. Postharvest product longevity is controlled by manipulating plant or product hormone **physiology** or by controlling respiration by lowering temperature or modifying environmental gas content.

fertigation application of small amounts of fertilizer while irrigating

hydroponic growing without soil, in a watery medium

physiology the biochemical processes carried out by an organism

The scientific and technological disciplines of horticulture include plant genetics, plant breeding, genetic engineering and molecular biology, variety development, propagation and tissue culture, crop and environmental physiology, plant nutrition, hormone physiology and growth regulation, plant physical manipulation (pruning and training), and environmental control. The crop disciplines of horticulture include pomology (fruit and nut culture), viticulture (grape production), enology (wine production), olericulture (vegetable culture), floriculture (flower culture) and greenhouse management, ornamental horticulture and nursery production, arboriculture (tree maintenance), landscape horticulture, interior plant scaping, turf management, and postharvest physiology, preservation, and storage. SEE ALSO AGRICULTURE, MODERN; BOTANICAL GARDENS AND ARBORETA; HORTICULTURIST; HYDROPONICS; ORNAMENTAL PLANTS; PROPAGATION.

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Horticulturist

A horticulturist practices the scientific or practical aspects of horticulture—growing, producing, utilizing, and studying horticultural crop plants and plant products. Careers in horticulture range from the scientific to the applied.

Careers in horticulture can be found in government (both state and national) agricultural research agencies, public and private universities, small companies, and multinational corporations. Jobs may entail laboratory work, greenhouse crop production and/or management, and field production. Research may involve developing and testing new products or technologies to improve the quality, appearance, handling, storage, or research and development of new plants or plant-derived products. Additional fundamental research is done to gain understanding of plant function, **physiology**, biochemistry, and genetics at the organismal, cellular, enzymatic, or molecular levels.

physiology the biochemical processes carried out by an organism

Horticulturists interested in teaching find employment at the high school, community school, vocational school, community college, or university levels. Emerging careers in horticulture include the study of plant-people interactions (the effects plants have on people), and horticulture therapy—the use of horticulture and gardening as a means of rehabilitation for those with physical, mental, or emotional limitations or challenges.

The practical or applied horticulturist is trained to utilize or manage plants and to design and maintain landscapes appropriately. Field horticulturists may be involved in the production of fruits and nuts (pomology), grapes (viticulture), and flowers and greenhouse crops (floriculture). They may also handle the arrangement, display, and marketing of cut flowers and

A horticulturist checks long-stemmed roses in a greenhouse.

greenery (floristry). Other possible areas of responsibility include the production of ornamental plants, trees, and shrubs (nursery production); landscape design, installation, and management; public or private garden installation and care; the design, installation, and maintenance of plants in indoor environments (interior plantscaping); turfgrass production, installation, and upkeep; and the handling, storage, and shipping of horticulture crops or plant products. The practical field horticulturist handles plant nutrition by fertilization, water status by irrigation, and plant size and shape by pinching, pruning, training, and mowing. Plant growth, development, and flowering is managed by the use of regulating chemicals or environmental management (temperature and light intensity and duration). The horticulturist is often the person primarily responsible for pest (both insects and disease) control and prevention management. Ultimately, the horticulturist is responsible for producing plants or plant products of the highest quality, value, and appearance.

Exciting developments in horticulture include the exploration of new plants as landscape greenery or for their potential medicinal contents and the discovery of wild types of cultivated crop plants such as strawberry, onion, tomato, or apple, which may contain genes for disease resistance or improved nutritional quality. Crops are being bioengineered for improved pest resistance, thereby requiring less pesticide in production, and being modified for increased storage life. Molecular biology and genetic engineering may result in the development of entirely new crops and/or the production of plants containing phyto-pharmaceuticals—plant-produced chemicals for use as beneficial drugs. Molecular biology and biochemistry are shedding new light on how plants grow and function, which will lead to new developments in crop production systems and management.

The level of employment and responsibility of a horticulturist relates to one’s amount of training, education, and experience. Horticultural training at the high school and vocational level typically involves work in plant management, production, and maintenance operations. At the college level, horticulturists receive fundamental education in plant science and biology as a foundation to understanding plant growth, development, and management. Typically, college curricula include strong training in science, including botany and plant anatomy/morphology, chemistry and biochemistry, genetics, physics, soil science, pest management, and plant physiology. Additionally, students receive training in the science and technology of horticulture, including greenhouse operations, nursery production, landscape design, landscape installation and management, fruit and vegetable production, and plant propagation. Students interested in pursuing scientific/technology development careers or those who wish to teach horticulture may continue college studies in a master’s or Ph.D. program.

Beginning horticulturists are typically responsible for plant management operations. Increased education, training, and experience result in increased decision-making and responsibility for operations and crew management. Entry-level positions with no training or experience begin at minimum wage, but with higher levels of training, experience, and increased ownership of an operation, salaries exceeded $100,000 per year. In 1999, students with a college degree found employment in the range of $25,000 to $40,000 for entry-level management positions. Salaries increase with experience gained through internships, fellowships, special research projects, travel, and part-time employment.

Horticulture production, education, and science careers can be found throughout the world. In the United States, primary horticulture production occurs in California, Florida, Texas, Georgia, Michigan, New York, Ohio, Pennsylvania, and New Jersey. However, landscape horticulture, retail garden center production, florist operations, public and private gardening, park landscape management, and landscaping design, installation, and maintenance operations flourish in all towns, cities, and metropolitan areas. International careers can be found through government and nongovernment agencies such as the Peace Corps, or with large multinational horticultural companies.

A commonality of horticulturists is, simply, that they enjoy working with plants. Horticulturists typically have a strong environmental ethic and enjoy contributing to beautifying and improving the environment and conserving natural resources. SEE ALSO ARBORIST; COLLEGE PROFESSOR; CURATOR OF A BOTANICAL GARDEN; CURATOR OF AN HERBARIUM; HORTICULTURE; LANDSCAPE ARCHITECT.

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Human Impacts

The human species has had a greater impact on the **biosphere** than any other single species. It is now poised to cause more changes in the future of the biosphere than even photosynthetic bacteria caused when they first filled the atmosphere with oxygen. While human impacts are as old as the human species itself, their pace and extent have grown rapidly, and recent changes have begun to dwarf the consequences of even the most profound change ever brought about by our species, the development of agriculture.

biosphere the region of the Earth in which life exists

The Coming of Agriculture

Until the development of agriculture, the human species did not affect the biosphere any more significantly than other highly efficient predators. While small nomadic groups could, and did, deplete local game populations, and could, and did, drive some species to the edge of extinction through overhunting, human impacts were for the most part small, local, and short-lived.

A Kansas wheat field being harvested. The ancient grasslands of the Midwest with the food chains they sustained have been replaced by agriculture

Agriculture changed all that. By cultivating and harvesting grains, humans set in motion a series of changes with deep effects on both the natural world and their own culture that have continued, and intensified, to this day. First and most profoundly, grains gave humans a source of surplus food that allowed population growth. While a surplus of meat would rot, a surplus of grain could be stored for months, even years, without losing its nutritional value. With a steady source of food supplied by plants, the human population began the extraordinary growth that continues exponentially in the twenty-first century.

Changes in the Landscape

The inexorable growth of the human population has caused significant impacts on the landscape everywhere humans have settled. For instance, before the coming of the Europeans in America, it is said that the eastern forests were so thick that a squirrel could travel from the Atlantic coast to the Mississippi River without ever setting foot on the ground. Less than two centuries later—a blink of the eye in evolutionary time—more than two-thirds of that forest had been cleared for pasture or plowing. While the earliest settlers feared the bears and the wolves that haunted their forests, by the nineteenth century, not even deer or beavers were found in central Massachusetts. (Remarkably, much of this has changed yet again. With the western movement of agriculture in the late 1800s and the general decline of farming in the northeast, much of the forest has returned, and that squirrel has a better chance of making its journey now than it did at any time in the last 150 years.)

But while part of the country has reverted somewhat to its forested past, much of the rest remains significantly altered by agriculture, especially in the Midwest. Here, the flat terrain and deep, rich soils combine to form an ideal region for growing grain. The ancient grasslands have mostly long since disappeared, and with them went the herds of bison and other animals that formed the food chain of the prairie. While eastern forests may have returned with the shift of agriculture to the Midwest, it is unlikely that the prairie will ever regain its predominance in turn—there simply is nowhere else for agriculture to move to in this country.

For Better or Worse

The Midwest is not the only region in which ancient food chains have been altered. In fact, it is estimated that almost 50 percent of the terrestrial net primary productivity of the Earth—almost one-half of all the photosynthesis carried out over the entire surface of the land—is consumed, wasted, or diverted by humans. In a very real sense, our species farms the entire planet. As the population expands in the twenty-first century, this number is expected to grow.

This harnessing of Earth's potential for our own purposes is not necessarily a bad thing, and how we view such transformations depends quite a lot on our own preconceptions about nature and the place of humans in it. Are buffalo better than cows? Are forests better than pastures? Throughout much of our history, most people have decided, consciously or not, that human need, and sometimes greed, is sufficient reason for wreaking change on the natural world. It is unarguably true that more people live in better conditions as a result of agriculture and all it has brought. Agricultural changes are, in any event, a fait accompli—the human species is simply not going to return to its hunting and gathering ways.

The Industrial Revolution

While agriculture has wrought slow, pervasive changes on human culture and the landscape over more than ten millennia, other human endeavors have had much faster impacts on Earth and its **biota**. The greatest of them all, and second only to agriculture in its overall impact, has been the Industrial Revolution. Beginning in the late 1700s with the invention of the steam engine and continuing through the twenty-first century, humans have harnessed increasing amounts of stored energy to drive larger, faster, and more powerful machines.

biota the sum total of living organisms in a region of a given size

The effects on the biosphere have been pervasive. Fuel-powered machines have allowed humans to cultivate more land, consume more resources, and sustain larger populations than was conceivable before the beginnings of this most important revolution. In addition to these effects, the use of fuel has had far-reaching consequences by itself. Wood-fired boilers soon gave way to coal, but not before deforestation of thousands of acres of virgin forests in the rapidly industrializing regions of Europe. Coal mining is a dirty business, and leaves in its wake scars on the landscape that can take generations to heal. More significantly, coal and its replacement, oil, are fossil fuels, the geologic remains of ancient plants that contain carbon removed from the carbon cycle millions of years ago. Burning fossil fuels releases carbon dioxide into the atmosphere, and records show the atmospheric level of CO_2 has risen steadily since the beginning of the Industrial Revolution. Carbon dioxide is a greenhouse gas, which traps heat in the atmosphere, preventing it from escaping into space. (Other greenhouse gases include methane and water vapor.) Deforestation raises CO_2 levels even more, since forests remove CO_2 from the air and lock it up in their woody tissues.

A piece of a Peruvian rain forest being converted for agricultural use by the slash-and-burn method.

Global Climate Change

While the chemistry and physics of the atmosphere are highly complex, and although there is still some debate about the pace and ultimate extent of global warming, most atmospheric scientists agree that the average temperature of the planet is likely to rise by at least a few degrees over the next several centuries. What portion of this effect is attributable to human activity is still under debate, although many scientists think the human contribution is very significant.

The scope of the possible effects of global warming is hard to forecast accurately, but some examples may provide a glimpse of potential outcomes. The current distribution of plant species is determined in large part by their climatic requirements. Boreal forest, or taiga, circles the Earth just below the arctic circle. Its coniferous trees require cold winters and mild summers, with moderate but not excessive rainfall. As surface temperatures rise, as much as 40 percent of the world's boreal forests could be lost, according to estimates published by the Intergovernmental Panel on Climate Change. At the same time, deserts and other arid lands may experience more water stress, increasing the rate of desertification in these regions. In contrast, some areas will become milder and wetter. All of these changes will shift plant geographic distribution, and with this, alter wildlife and plant predator distributions.

Invasive Species

Changes in climate are likely to accelerate another trend, one already begun by humans in their global travels. The distribution of plants changes over time, but in most natural migrations, predators move along with the plant, providing checks on the potential for otherwise explosive growth into a new habitat. When humans deliberately introduce a foreign plant into a new habitat, however, the system of ecological controls is not often transplanted at the same time. In these situations, a new species may have a significant impact on local **ecosystems**, driving out indigenous species and altering balances in place for many years. Such has been the case, for instance, with purple loosestrife in eastern wetlands, melaleuca in the Everglades, and kudzu throughout the southern United States.

ecosystem an ecological community together with its environment

As temperature and rainfall patterns change, global climate change is likely to provoke the large-scale introduction of new species into ecosystems where they have never existed before. A significant unanswered question is whether these changes are likely to be slow, allowing time for species to migrate gradually and for communities to slowly adapt to new constellations of species, or whether change will come rapidly, causing extinction of some species too slow to migrate, and population explosions of others that outpace their predators in a new environment. The rate of climate change, as well as its extent, will have a significant impact on the characteristics of plant communities in the twenty-first century.

The Sixth Extinction

While species have become extinct at a small, steady rate throughout evolutionary time, the three-and-a-half-billion-year history of life has been punctuated by only five great extinction events, most caused by heavenly cataclysms, such as an asteroid colliding with Earth. We are now in the early stages of the sixth great extinction, but one with a difference—this cataclysm is entirely of human origins.

This wave of extinction is perhaps the most alarming, and most grim, of the impact humans have had on the biosphere. By some estimates, one in eight species of plants is on the edge of extinction, and most of these were not expected to survive into the twenty-first century. Similar predictions have been made for other life forms. Human activities have increased the extinction rate by a thousand-fold, so that for every new species created by evolution, one thousand become extinct through the effects of human activities. Expanding populations, pollution, and atmospheric ozone depletion all have played their part, but the most dramatic effect has come from the clearing of tropical rain forests for agricultural and lumber activities. Forest clearing in tropical areas destroys 86,000 acres of forest per day, and an area the size of Kansas every year. With this land go thousands of species, many of them never identified.

The loss of these species is significant for practical as well as bioethical reasons—the unique biochemistry of each species makes each a potential source for new drugs or raw materials with unique and valuable properties. Plants are especially valuable in this regard, since their inability to run away from predators has led to the evolution of many types of bioactive **compounds**, only now being discovered by plant prospectors and

compound a substance formed from two or more elements

ethnobotanist a scientist who interacts with native peoples to learn more about the plants of a region

biodiversity degree of variety of life

ethnobotanists. Destroying this inventory before even cataloging potentially throws away our future.

Future Prospects

The enormity of human impacts on the biosphere—increasing global temperatures, decreasing **biodiversity**, higher populations—is sometimes enough to make one despair of changing anything. While it is true that the major outlines of the future are unlikely to be reversed in the next several decades, it is most definitely not true that inaction is the only sensible course. Many important steps have already been taken to steer a course toward a more sustainable environmental future. While political differences and short-sighted economic interests will continue to prevent the full range of international actions needed, heartening agreements are already in place to decrease ozone destruction, limit greenhouse gas emissions, and protect biodiversity. The world's people and its political leaders are slowly understanding that the future health and prosperity of the human species depends critically on the health of the world's environments.

Despite these promising beginnings, a great deal remains to be done, and the doing of it will depend on the commitment and foresight of people like the readers of this book, who are willing to learn, get involved, and try to make a difference. In the twenty-first century, that commitment to make a difference may have the greatest impact of all. SEE ALSO Acid Rain; Agriculture, History of; Agriculture, Modern; Atmosphere and Plants; Biogeochemical Cycles; Bioremediation; Boreal Forest; Carbon Cycle; Deforestation; Ecology, Fire; Genetic Engineering; Global Warming; Grasslands; Green Revolution; Invasive Species; Rain Forests.

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Humboldt, Alexander von

German Explorer and Scientist
1769–1859

continental drift the movement of continental land masses due to plate tectonics

Alexander von Humboldt.

Alexander von Humboldt was the greatest explorer-scientist of the eighteenth and early nineteenth centuries. Humboldt's contributions to science were remarkably diverse. He was the first person to map areas of equal air temperature and pressure, a technique now used in every weather forecast around the world. By measuring the magnetism of rocks in the Alps, he found that Earth's magnetic field reverses its polarity. This fundamental discovery allowed geologists in the twentieth century to prove the theory of **continental drift**. Humboldt also developed the idea of seismic waves that travel through Earth's surface after an earthquake. In physics, he conducted more than four thousand experiments on electricity and magnetism. Perhaps his most important research, however, concerned the distribution and environmental relationships of plants.

Humboldt's interest in botany developed early on. While a teenager he spent many hours with Karl Willdenow, one of the leading botanists in Europe, collecting and classifying plants in the woods around Berlin. In 1789, while studying at the University of Gottingen, Humboldt met Johann Forster. Forster had accompanied James Cook on a voyage around the world and was one of the best naturalists of his day. On expeditions with Forster to France, England, and the Netherlands, Humboldt learned the techniques of scientific observation, plant classification, and precise measurement that he would employ throughout his long and incredibly productive career.

In 1790, Humboldt began work in plant geography that would revolutionize botany. Humboldt's botanical work was greatly influenced by German natural philosophers such as Immanuel Kant. Kant believed that there was an underlying causal unity in nature and that Earth should be viewed as a single, interconnected whole. Extending these ideas to the study of plants, Humboldt sought to create a universal, **holistic** science of botany that encompassed both the diversity and connectedness of the natural world. In his words: "Science can only progress . . . by bringing together all of the phenomena and creations that the earth has to offer . . . nothing can be considered in isolation . . . . Nature, despite her seeming diversity, is always a unity."

holistic including all the parts or factors that relate to an object or idea

By 1797 Humboldt had become bored with his work in geology at the German Ministry of Mines. "I was spurred by an uncertain longing for the distant and unknown," he wrote. "For . . . danger at sea . . . the desire for adventures." On June 5, 1799, accompanied by his colleague, the botanist Aimé Bonpland, Humboldt embarked on an expedition to South America to "find out how the geographic environment influences plant and animal life." Landing in Cumana, Venezuela, Humboldt spent the next five years exploring uncharted regions of the Oronoco River, Colombia, Peru, and Ecuador.

During this journey, Humboldt survived attacks by Native Americans, tropical disease, starvation, near drowning in capsized canoes, and shocks from electric eels. Despite incredible hardships, he carried out meticulous observations on South American plants, geography, geology, climate, Aztec art, and native languages. In Ecuador, he mapped the **zonation** of vegetation on mountain sides and correlated this zonation with climatic changes. In Venezuela, anticipating the field of conservation biology, he analyzed complex relationships between logging, river ecology, and erosion. These fundamental studies of the relationships between plants and their environment laid the foundation for the emergence of the science of ecology during the nineteenth century. SEE ALSO BIOGEOGRAPHY; ECOLOGY, HISTORY OF; PLANT COMMUNITY PROCESSES.

zonation division into zones having different properties

Bradford Carlton Lister

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Hybrids and Hybridization

Three varieties of grain: rye, triticale, and wheat.

Hybridization is generally defined as the interbreeding of individuals from two populations or groups of populations that are distinguishable on the basis of one or more heritable characters. By extension, a hybrid is an individual resulting from such interbreeding. Hybrid zone refers to a region in which hybridization is occurring. Artificial hybridization refers to instances in which these crosses occur under controlled conditions, often under the direction of plant or animal breeders. In contrast, natural hybridization involves matings that occur in a natural setting.

Factors Limiting Natural Hybridization

A variety of factors serve as reproductive barriers among plant **taxa**. These barriers, which can be subdivided into those acting prior to fertilization (prezygotic) or following fertilization (postzygotic), restrict natural hybridization and help maintain species boundaries.

taxa a type of organism, or a level of classification of organisms

Prezygotic Barriers. The potential for natural hybridization is largely determined by the proximity of potential mates in both space and time. The likelihood of hybridization is therefore governed, to a large extent, by differences in the ecology (spatial isolation) and/or phenology (temporal isolation) of the individuals of interest. Even if ecological and temporal differentiation are absent, pollen transfer may be limited by differences in floral morphology (form). Differences in traits such as floral color, fragrance, and nectar chemistry can influence pollinator behavior and may discourage the transfer of pollen among different species (ethological isolation). Alternatively, the structure of the flower may preclude or limit pollination of one taxon by the pollinator(s) of others (mechanical isolation). Finally, even if pollen transfer is successful, the pollen may not germinate on a foreign stigma; if it does, the pollen tubes may fail to effect fertilization due to slow growth or arrest prior to reaching the ovule (cross-incompatibility).

Postzygotic Barriers. Assuming that fertilization occurs, the resulting hybrid progeny (offspring) may fail to survive to reproductive maturity due to developmental aberrations (hybrid inviability). If the hybrids do survive, their flowers may be unattractive to pollinators, thereby restricting further hybridization (floral isolation). Alternatively, the hybrids may be attractive to pollinators but partially or completely **sterile** (hybrid sterility). Finally, even if first generation hybrids are viable and fertile, later-generation hybrids may exhibit decreased levels of viability and/or fertility (hybrid breakdown).

sterile unable to reproduce

History of Investigations

The scientific study of hybridization dates back to Carolus Linnaeus (1707–1778). In 1757, as part of an investigation as to whether or not plants reproduce sexually, Linnaeus produced hybrids between two species of goats-beard (*Tragopogon porrifolius* and *T. pratensis*). Although this work served primarily as proof of the sexual nature of reproduction in flowering plants, Linnaeus argued that "it is impossible to doubt that there are new species produced by hybridization generation." Shortly thereafter, Joseph Gottlieb Kölreuter (1733–1806) revealed two important flaws in Linnaeus's conclusions. Kölreuter first showed that hybrids from interspecific crosses are often sterile "botanical mules," a result that led him to conclude that hybrids are difficult to produce and unlikely to occur in nature without human intervention or habitat disturbance. He went on to demonstrate that, although early generation hybrids are often **morphologically** intermediate to their parents, later generation hybrids tend to revert back to the parental forms. This finding apparently refuted Linnaeus's earlier suggestion that hybrids were constant or true-breeding and represented new species.

morphologically related to shape or form

In the latter part of the eighteenth century through the nineteenth century, hybridization techniques were widely applied to plant and animal breeding, a focus that continues today. The utility of hybridization for breeding programs lies in the fact that first-generation hybrids often exceed their parents in vegetative vigor or robustness. This phenomenon, known as hybrid vigor or heterosis, has been used to maximize yields in crop plants. Early botanists were also interested in the validity of hybrid sterility as a species criterion. This work was accompanied by increasingly frequent reports of natural hybrids between wild plant species. There was, however, little discussion of an evolutionary role for hybridization during this period, although sporadic reports of true-breeding hybrids continued to surface.

In the mid-nineteenth century, Gregor Johann Mendel (1822–1884) used hybridization to solve the problem of heredity. By analyzing the hybrid progeny of crosses between distinct varieties of garden pea (*Pisum sativum*), Mendel was able to demonstrate that genetic information is passed from one generation to the next in discrete units, and that these units (later known as genes) exist in pairs (later known as **alleles**). This work, which went largely undiscovered until 1900, provided a framework for the development of modern genetics.

allele(s) one form of a gene

Importance of Hybridization

In the early twentieth century, three key discoveries laid the foundation for modern evolutionary studies of hybridization. The first discovery was by Øjwind Winge (1886–1964), who showed that new, true-breeding hybrid species could be derived by the duplication of a hybrid's chromosome complement (i.e., allopolyploidy). A second important discovery resulted from the work of Arne Müntzing (1903–1984), G. Ledyard Stebbins (1906–2000), and Verne Grant (1917–) on the possible origin of a new species via hybridization without a change in chromosome number (i.e., homoploid hybrid **speciation**). A third key advance resulted from studies of natural hybrid populations by Edgar Anderson (1897–1969) and coworkers. Anderson suggested that interspecific hybrids might be favored by natural selection and thus contribute to the formation of **intraspecific taxa** such as varieties or subspecies.

speciation creation of new species

intraspecific taxa levels of classification below the species level

Allopolyploid Hybrid Speciation. Polyploidy refers to the situation in which an organism carries more than two full chromosomal complements. When the chromosome complements come from different species, these individuals are referred to as allopolyploids. **Allopolyploidy** is without a doubt the most frequent solution to the problems of hybrid sterility and segregation. In its simplest form, **genome** duplication in hybrids leads to the formation of fertile allopolyploids. This most commonly occurs via the fusion of unreduced (**diploid**) gametes.

allopolyploidy a polyploid organism formed by hybridization between two different species or varieties (*allo* = other)

genome the genetic material of an organism

diploid having two sets of chromosomes, versus having one (haploid)

Allopolyploidy has several consequences that are relevant to hybrid speciation. First, it may lead to instantaneous reproductive isolation between the new allopolyploid species and its diploid parents. Crosses between **tetraploid** and diploid individuals, for example, will produce triploid offspring that are partly or completely sterile due to the presence of unpaired chromosomes in meiosis. Second, genome duplication can generate biochemical, physiological, and developmental changes, giving polyploids ecological tolerances that are quite different from those of their diploid **progenitors**. Altered ecological preferences increase the likelihood of successful establishment of an allopolyploid because it need not compete directly with its diploid parents. Third, genome duplication provides a means for stabilizing the hybrid vigor often associated with first-generation hybrids. This also contributes to the evolutionary potential of a newly arisen allopolyploid species. Finally, genome duplication promotes a series of genetic and chromosomal changes that increases the differences between the polyploid species and its diploid progenitors. These include the loss of deoxyribonucleic acid (DNA), the silencing or divergence of duplicated genes, and the increase in frequency of alleles that perform best in a polyploid genetic background.

tetraploid having four sets of chromosomes; a form of polyploidy

progenitor parent or ancestor

Homoploid Hybrid Speciation. The evolutionary conditions required for homoploid hybrid speciation are much more stringent than for allopolyploidy. Unlike allopolyploids, homoploid hybrids are not instantaneously reproductively isolated from their parents (because the chromosome number remains the same), and new hybrid **genotypes** are likely to be lost though matings with their parents. Thus, models for homoploid hybrid speciation must explain how a new hybrid genotype can become reproductively isolated from its progenitor species.

genotype the genetic makeup of an organism

The most widely accepted model of homoploid hybrid speciation is the recombinational model of Stebbins and Grant. In this model, the genes or chromosomal rearrangements responsible for hybrid sterility are assumed to assort in later generation hybrids to form lineages characterized by a new combination of sterility factors. The new hybrid lineages would be fertile and stable yet partially reproductively isolated from their parents by a sterility barrier. Although early authors focused on evolution of sterility barriers, naturally occurring hybrid species appear to have become isolated from their parental species by both ecological divergence and sterility barriers. Thus, models of this process now incorporate both ecological and genetic isolation. Modern contributions to the study of this process include rigorous experimental and theoretical tests of the model, as well as the gradual accumulation of well-documented case studies from nature.

Introgressive Hybridization. As discussed above, the development of reproductive isolation represents a major challenge for the origin of homoploid hybrid species. Thus, it is perhaps not surprising that intraspecific taxa such as varieties, ecotypes, or subspecies more commonly arise via **interspecific hybridization** than do fully isolated hybrid species. The process by which intraspecific taxa arise via hybridization is straightforward. In natural hybrid zones, interspecific hybridization is often followed by backcrossing to one or both parental species. This process is referred to as introgression, and it produces hybrid offspring that largely resemble one of the parental species, but also possess certain traits from the other parental species. If the hybrid gene combinations become fixed, the resulting hybrid products are referred to as

interspecific hybridization hybridization between two species stabilized introgressants. As with allo- and homoploid hybrid species, most stabilized introgressants are ecologically divergent with respect to their parental species. Thus, ecological divergence appears critical to successful establishment; otherwise, new introgressants are likely to be eliminated by competition and/or gene flow with parental populations. Although molecular markers have been used since the 1970s to document introgressive races and subspecies in many groups of plants and animals, the overall contribution of introgression to adaptive evolution remains poorly understood. SEE ALSO Breeding; Burbank, Luther; Cultivar; Evolution of Plants; Phylogeny; Polyploidy; Speciation; Species; Taxonomy.

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Hydroponics

Hydroponics is the practice of growing plants without soil. Plants may be suspended in water or grown in a variety of solid, **inert** media, including vermiculite (a mineral), sand, and rock wool (fiberglass insulation). In these cases, water that permeates the medium provides the nutrients, while the medium provides support for root structures. Hydroponics allows precise control of nutrient levels and oxygenation of the roots. Many plants grow faster in hydroponic media than in soil, in part because less root growth is needed to find nutrients. However, the precise conditions for each plant differ, and the entire set up must be in a greenhouse, with considerable investment required for lights, tubing, pumps, and other equipment.

inert incapable of reaction

Sprouts growing in a hydroponic hot house in Japan.

While hydroponics is as old as the hanging gardens of Babylon, modern hydroponics was pioneered by Julius von Sachs (1832–1897), a researcher in plant nutrition, and hydroponics is still used for this purpose. It is also used commercially for production of cut flowers, lettuce, tomatoes, and other high-value crops, although it still represents a very small portion of the commercial market. SEE ALSO AGRICULTURE, MODERN; ROOTS; SACHS, JULIUS VON.

Richard Robinson

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Identification of Plants

All known plant species have names. Unfortunately, outside of flower shops and botanical gardens, they do not come with nametags. Therefore, it is often necessary to identify an unknown plant, that is, to determine the species to which it belongs and thus its name. Identification assumes that the plants have already been classified and named. When you identify a plant, you are basically asking: "Of all known species, which one most closely resembles this individual in my hand?"

Professionals and serious amateurs identify plants by keying. This is a stepwise process of elimination that uses a series of paired contrasting statements, known as a dichotomous key. Keying is like a trip down a repeatedly forking road: If at the first fork you turn right, you cannot possibly reach any of the towns that lie along the left fork. Each successive fork in the road eliminates other towns, until you finally reach your destination.

When keying, the user begins by reading the first pair of statements (called a couplet). For example, a key may begin by asking the user to decide between "plants woody" and "plants not woody." If the unknown is woody, all nonwoody species are immediately eliminated from consideration. Successive couplets will eliminate further possibilities until only one remains, which is the species to which the unknown must belong. The advantage of this procedure is that the user must only make one decision at a time, rather than mentally juggling long lists of features of many possible candidates.

specimen object or organism under consideration

Once the plant has been keyed, it is necessary to confirm the identification. Most books that include keys also include detailed descriptions; some also include illustrations of all or selected species. If the **specimen** that was keyed matches the appropriate description and/or illustration, the identification may be assumed to be correct. If one has access to an herbarium, the specimen that was keyed can be compared to previously identified specimens of the species as a further check of the identification.

Although plant classifications are based upon information from many disciplines, including genetics, chemistry, and molecular biology, identification almost always relies on readily observed structural features, both vegetative and reproductive. For this reason, it is essential that specimens for identification be as complete as possible. Those of small plants should include not only all aboveground portions but also the roots. For large woody plants, a fully expanded twig of the current season will suffice. In all cases, specimens must include reproductive structures (i.e., flowers, fruits, seeds). Features that are not represented in the physical specimen (e.g., height or girth of trees, features of the bark, colors or odors that fade in drying) should be noted at the time of collection.

Equipment requirements to identify plants are few: a magnifying lens of 10 to 300 power, a 10-centimeter ruler, simple dissecting tools (forceps, teasing needles, razor blades), and a key. An excellent bibliography of appropriate keys for plants of all parts of Earth is provided by Frodin (1983). As for personal requirements, the most important is a critical eye, that is, the ability to observe carefully and to correctly interpret what is observed. This requires some familiarity with both plant structures and the terminology used to describe them. A comprehensive resource for this topic is Radford's introductory textbook (1986). Above all, as with most skills, there is no substitute for plenty of practice. SEE ALSO FLORA; FLOWERS; HERBARIA; INFLORESCENCE; SYSTEMATICS, MOLECULAR; SYSTEMATICS, PLANT; TAXONOMIC KEYS; TAXONOMY.

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Inflorescence

An inflorescence is a collection of flowers in a particular branching pattern that does not contain full-size leaves among the flowers. While there are many kinds of inflorescences to be found in flowering plants (angiosperms), each species has its own form of inflorescence, which varies only minimally in individual plants. However, if a plant bears only a single flower, or makes many single flowers scattered on a tree with interspersed leaves, no inflorescences are said to be present.

Inflorescences (sometimes called flower stalks) can be divided into two main categories, with many types within each. These two categories are determinate and indeterminate, and can be distinguished by the order in which the flowers mature and open. Determinate inflorescences mature from the top down (or the inside out, depending on the overall shape of the inflorescence). In other words, the oldest and therefore largest flowers (or flower buds) on a determinate inflorescence are located at the top (or center) while the youngest flowers can be found at the bottom (or outside edge). Thus, the flowers mature from the top down (or the inside out). The situation is reversed for indeterminate inflorescences: the youngest flowers are at the top and the oldest flowers are found at the bottom. Flowers in an indeterminate inflorescence mature from the bottom up (or the outside in). The terms determinate and indeterminate refer to the potential number of flow-

A flowering rush (*Butomus umbellatus*) displays its umbel of pink to red flowers.

ers produced by each inflorescence. In a determinate inflorescence, the number of flowers produced is determined by the manner in which the inflorescence is put together. An indeterminate inflorescence can continue to produce more flowers at its tip if conditions are favorable and are thus more flexible in flower number.

Each of the two broad categories of inflorescences can be divided into specific types. For the indeterminate inflorescences, the simplest types are the spike, raceme, umbel, panicle, and head. The spike has a single unbranched stem with the flowers attached directly to the stem. A raceme is similar, but the flowers each have their own short stems, which are attached to the main stem. An umbel has flowers with stems that all attach out in the same point on the main stem, resulting in an umbrella-like appearance that can be flat-topped or rounded. Panicles are highly branched with small individual flowers. A head typically has very small individual flowers that are collected in a densely arranged structure; sunflowers and daisies are good examples. Determinate inflorescences tend to be more branched and include the cyme, dichasium, and corymb. A cyme is a branched inflorescence where all flower **pedicels** and branches originate at the same point. A dichasium is more elongated and a corymb is flat-topped. All of these basic types can be further modified in shape and/or reiterated, resulting in complex inflorescences that can be very difficult to identify.

pedicel a plant stalk that supports a fruiting or spore-bearing organ

Inflorescences serve as a way for a plant to maximize its reproductive success. Flowers are collected into showy structures to better attract pollinators, to increase seed production, or aid in seed dispersal. Inflorescences can result in platforms suitable for insects or birds to land upon. Some inflorescences are tough and protect the floral parts from damage from the elements or from pollinating mammals. SEE ALSO ANATOMY OF PLANTS; FLOWERS.

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Ingenhousz, Jan

Dutch Physician
1730–1799

Jan Ingenhousz.

Jan Ingenhousz made major contributions to plant **physiology** as well as human medicine. He was born in the Netherlands, received a medical degree in 1753, and went on to further study in Leiden, Paris, and Edinburgh, finally aiding in the discovery of a new smallpox inoculation procedure. For a time he lived in England, where he befriended Benjamin Franklin and Joseph Priestley. After his success with the smallpox vaccine, however, Empress Maria Theresa of Austria called Ingenhousz to the Austrian court. There he served as personal physician to the empress for twenty years. He returned to in England in 1778.

physiology the biochemical processes carried out by an organism

Ingenhousz had an early interest in gases, which led to his interest in photosynthesis. The results of his work demonstrated both the disappearance of gas and the production of oxygen during photosynthesis. Ingenhousz disproved the belief that carbon comes from the soil by establishing a relationship between photosynthesis and plant respiration, claiming that the carbon used by plants came from the carbon dioxide in the air. In addition, he showed that only green leaves have the ability to purify the air through photosynthesis.

In 1778 Ingenhousz conducted experiments on plant production of oxygen. He showed that the green leaves of plants must be exposed to substantial daylight for oxygen production to occur. From this result, he was able to counter the arguments and statements of his contemporary chemists regarding the source of oxygen. Ingenhousz began applying many of the techniques pioneered by Priestley to the study of plant respiration. Priestley had designed a mechanism for measuring oxygen called a eudiometer. Nitric oxide was injected into a closed vessel in which there was already water. A reaction would then occur between nitric oxide and the oxygen in water, producing nitrous dioxide, which is soluble in water. Therefore, the amount of oxygen in the water could be measured by watching the water in the vessel rise.

Using this technique, Ingenhousz showed that plants need the presence of light in order to purify air. In the presence of light, he concluded that "all plants possess a power of correcting, in a few hours, foul air, unfit for respiration; but only in clear light, or in the sunshine."

After he had made this conclusion (what we now call carbon fixation), Ingenhousz began thinking about ways in which oxygen might help respiratory patients; he built some equipment for this purpose but never got terribly far.

In addition to his work on carbon fixation, Ingenhousz performed substantial particle research using algae **specimens**. His research on algae led to his preliminary observations of what would later be called Brownian

specimen object or organism under consideration

Motion and illustrated that lifeless particles show motion. Notably, Ingenhousz was also the first to use thin glass coverslips for liquid preparations viewed under microscopic lenses. SEE ALSO Atmosphere and Plants Photosynthesis, Carbon Fixation and; Photosynthesis, Light Reactions and; Physiologist; Physiology; Physiology, History of.

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Interactions, Plant-Fungal

Fungi are the most common parasites of plants, causing many kinds of diseases. Nonetheless, a fungus often parasitizes a plant without causing harm, and it may even be beneficial. Two well-known examples of beneficial fungi are the mycorrhizae and fescue endophytes.

A mycorrhiza is a fungus-root association in which the fungus infects the root without causing harm. In fact, the plant often benefits because the fungal **hyphae** in the soil obtain mineral nutrients that are some distance from the root. Ectomycorrhizae are commonly found on both hardwood and coniferous trees in the forest or yard. A fungal mantle covers the root, and a network of hyphae can be found between cells in the root cortex. A special benefit of this mycorrhiza is that **pathogens** cannot penetrate the root. Many different fungi may serve as the fungal **symbiont**. A mushroom or puffball in the forest may be evidence of an ectomycorrhizal association.

hyphae the threadlike body mass of a fungus

pathogen disease-causing organism

symbiont one member of a symbiotic association

Vesicular-arbuscular (VA) mycorrhizae are common in crop plants all over the world. These endomycorrhizae have no fungal mantle but have extensive hyphae in the root cortex. Many branched hyphal structures called arbuscules invade cells and obtain food. The vesicles, ball-like structures found between **cortical** cells, seem to serve in food storage. The VA mycorrhizal fungi are all closely related and obligate parasites.

cortical relating to the cortex of a plant

endophyte a fungus that lives within a plant

The tall fescue **endophyte** *Acremonium* is a parasite that does not harm the plant. However, the infected grass is toxic to cattle. Endophyte-infected plants benefit by having greater stress tolerance and resistance to attack by insects. Endophyte-infected fescue is already being used as turfgrass, where the benefits can be realized without fear of toxicity to cattle. This character is readily maintained since the endophyte fungus is transmitted through the seed. SEE ALSO Chestnut Blight; Dutch Elm Disease; Interactions, Plant-Insect; Mycorrhizae; Pathogens; Potato Blight.

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Budded hyphae magnified two hundred times.

Interactions, Plant-Insect

Insect-plant interaction refers to the activities of two types of organisms: insects that seek out and utilize plants for food, shelter, and/or egg-laying sites, and the plants that provide those resources. These interactions are often examined from the plant's perspective, and a principal broad research question is: "How do the activities of the insect affect plant growth and development?"

The interactions can be beneficial to both the plant and the insect, as illustrated by pollination. During pollination, an insect moving within a flower to obtain nectar may transfer pollen either within that flower or among other flowers on that plant. Other relationships between insects and plants can be detrimental to the plant but beneficial to the insect (e.g., herbivory, or feeding upon the plant). Plant-feeding insect species are numerous, constituting more than one-quarter of all **macroscopic** organisms. Although most plant parts are fed upon by insect **herbivores**, the majority of insect herbivores are specific in terms of the plant species and the plant part on which they will feed. Some examples of significant insect herbivores

macroscopic large, visible

herbivore an organism that feeds on plant parts

Tent caterpillars crawl across a silken web that covers a tree branch and its leaves.

worldwide on cultivated crops include: aphids on cereal crops, diamondback moth larvae (immatures) on members of the cabbage family, and larvae of the moth genus *Heliothis* on a broad range of plants, including cotton. In addition to the direct effects of herbivory, insects can be damaging to plants by acting as vectors (carriers) of pathological microorganisms, transmitting the organisms when the insects feed on the plants.

Interactions in Agricultural Settings

In order to prevent significant losses of agricultural crops to herbivory, both in the field and following harvest, some form of insect population control is often required; some crops may require protection from more than one insect herbivore. Under conventional farming methods in the industrialized world, insecticides are applied to agricultural fields to control insect pests. Often, more than one type of insecticide and/or more than one treatment will be applied in a single crop cycle. The type of control method used for a particular insect/crop combination in part depends upon the understanding of the insect and its use of a particular crop plant. Research into novel aspects of insect-plant interaction may provide improved alternatives for controlling insect pest populations. For instance, recent research examining the effects of moth larvae feeding on corn has demonstrated that after herbivore damage, corn plants release a new complex of **odorants** into the air, and that some of these molecules are attractive to parasitic wasps. The parasitic wasps then seek out and parasitize the larvae feeding on the

odorant a molecule with an odor

corn plants. These odorants have the potential to be used to help control moth damage on corn.

A very different view of insect-plant interaction focuses on the use of insects as biological control agents for weeds and takes advantage of the fact that insects can feed destructively on plants. A well-known example of insect control of weeds occurred in Australia when prickly pear cacti were controlled by the cactus moth from Argentina, *Cactoblástis cactòrum* (Berg), an insect herbivore imported for that purpose.

Areas of Inquiry

Some insect-plant relationships can be traced through the fossil record, as some fossilized leaves show evidence of ancient herbivory that occurred prior to the fossilization of the plant material. Other insect-plant relationships continue to develop as insect species incorporate novel host plants into their diets and plants evolve new defensive compounds. The dynamic nature and variety of these interactions provides much opportunity to increase our understanding of the **physiology** of both types of organisms, interactions between them, and ecological and evolutionary processes.

physiology the biochemical processes carried out by an organism

Wendy Mechaber

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Interactions, Plant-Plant

In plant communities each plant might interact in a positive, negative, or neutral manner. Plants often directly or indirectly alter the availability of resources and the physical habitat around them. Trees cast shade, moderate temperature and humidity, alter penetration of rain, aerate soil, and modify soil texture. Plant neighbors may buffer one another from stressful conditions, such as strong wind. Some plants make contributions to others even after they die. Trees in old-growth forests that fall and decompose ("nurse" logs) make ideal habitat for seeds to sprout, and such a log may be covered with thousands of seedlings. While effects on the physical habitat are consistent aspects of communities, plant-to-plant competition to preempt resources also takes place, and in some instances chemical interactions occur between species.

Commensalism occurs as one species lives in a direct association with another (the host), gaining shelter or some other environment requisite for survival and not causing harm or benefit to the host. Orchids and bromeliads (*Neoregelia* spp.) live on the trunk or branches of their host, gaining water and nutrients from the air or bark surface without penetrating host tissue. Stocky roots and **xeromorphic** leaves that help gain and retain water are characteristic of **vascular** epiphytes (*epiphyte* means to live upon another). Bryophyte, lichen, and fern epiphytes are so abundant in the tropical rain forest that they often embody more plant material than their host trees. Another facilitation is illustrated by seedling growth of the Saguaro cactus (*Cereus giganteus*), which typically occurs in the shade of paloverde trees or

commensalism a symbiotic association in which one organism benefits while the other is unaffected

xeromorphic a form adapted for dry conditions

vascular related to transport of nutrients

A strangler fig tree, an example of a parasitic plant-plant interaction harmful to the host.

other plants, which create a better water-relationship environment for the cactus and protect it from the negative effects of the intense sun. Farming practices often use "nurse" plants to create a temporary improvement in the environment for the main crop. For example, oat and alfalfa may be seeded together so that oat shades and maintains better soil surface moisture for the emerging alfalfa seedlings.

legumes beans and other members of the Fabaceae family

Direct plant-plant contacts that benefit both organisms are termed mutualism. Taking the broader view of plants to include microorganisms, a good example of this arrangement is the association of **legumes** and nitrogen-fixing bacteria that live within legume root nodules. The legume benefits by obtaining nitrogen from the bacteria, while the bacteria gain necessary carbohydrate energy from legume photosynthesis. The free-living bacteria actually change and become bacteroids, no longer able to live outside the roots. The vast majority of higher plants have fungal-root associations called mycorrhizae. The vascular plants benefit because the fungus is much better at absorbing and concentrating phosphorus (and perhaps other mineral nutrients) than the root tissue, while the fungus gains a source of carbon compounds from the plant.

Parasitic plant-plant interactions are harmful to the host. A number of plants (e.g., dodders, broomrakes, and pinedrops) do not contain chlorophyll and cannot photosynthesize. They parasitize green plants by penetrating the outer tissue of the host plant with haustoria (rootlike projections), which eventually tap the water and food-conducting tissue. Mistletoe also form haustoria but the primary function of these structures is obtaining water, as this partially parasitic plant is capable of manufacturing its own food by photosynthesis. Witchweed (*Striga* spp.) has green leaves but is an **obligate** parasitic weed that causes tremendous crop losses to tropical-origin cereal grain crops and legumes. Witchweed has evolved so that chemicals from the host plant have become signals for witchweed seed to germinate and attach to the host. Subsequently, witchweed penetrates the host roots and steals water, minerals, and hormones. Strangler fig is a tree that germinates high in the host tree and sends roots to the ground, eventually killing the host when the fig roots and vines surround and strangle the flow of sugars in the host.

obligate required, without another option

It is rare that plants are unaffected by neighboring plants. Negative effects on one of the neighbors are referred to as interference, and they include competition and **allelopathy**. Competition, the situation in which one plant depletes the resources of the environment required for growth and reproduction of the other plant, is the most common plant-plant phenomenon in nature. Members of plant associations that are more successful at gaining major resources—water, nutrients, light, and space—have the advantage and typically dominate the community. Competitive advantage may result from a plant's season of growth, growth habit, or **morphological** features such as depth of rooting, and special physiological capabilities like differences in rate of photosynthesis. In contrast to competition, allelopathic interference is the result of a plant adding toxic chemicals to the environment that inhibit the growth and reproduction of associated species or those that may later grow in the area. Many negative effects on target species probably occur from a combination of competition and allelopathy. Chemicals released from one plant may also be a communication to other plants, causing germination (e.g., *Striga*) or signaling defense responses to insect attack. SEE ALSO ALLELOPATHY; DEFENSES, CHEMICAL; ECOSYSTEM; INTERACTIONS, PLANT-FUNGAL; INTERACTIONS, PLANT-INSECT; INTERACTIONS, PLANT-VERTEBRATE; INVASIVE SPECIES; MYCORRHIZAE; NITROGEN FIXATION; PARASITIC PLANTS; PLANT COMMUNITY PROCESSES; SYMBIOSIS.

allelopathy harmful action by one plant against another

morphological related to shape

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Interactions, Plant-Vertebrate

Because plants can photosynthesize, they form the base of food chains in most **ecosystems**. During the past five hundred million years, vertebrates have evolved many methods of extracting energy from plants, which can have positive or negative impacts on individual plants and their populations.

ecosystem an ecological community together with its environment

A bronzy hermit hummingbird (*Glaucis aenea*) sips from a red passion flower (*Passiflora vitifolia*).

frugivory eating of fruits

herbivore an organism that feeds on plant parts

avian related to birds

Positive interactions between plants and animals are called mutualisms. Familiar examples include pollination and **frugivory**, in which plants provide flowers containing nectar, pollen, and fruits with a fleshy pulp as food for animals, while animals disperse plant's pollen and seeds. Major vertebrate pollinators include a wide variety of birds (e.g., hummingbirds, orioles, and sunbirds) and many plant-visiting bats. Similarly, frugivorous vertebrates, including many kinds of birds, bats, and primates (and even certain fish in the Amazon River), consume fleshy fruits and move seeds to new locations. Many species of tropical trees and shrubs rely exclusively on vertebrates for pollination and/or seed dispersal.

In contrast, many vertebrates interact negatively with plants as **herbivores** and seed-eaters. Herbivory, which involves the consumption of leaves, roots, and stems, can reduce plant growth rates and seed production if it does not kill plants outright. Seed predation, in which animals destroy plant embryos, is a specialized form of herbivory. Herbivory is much more common in mammals than in birds. Ptarmigan and grouse are **avian** herbivores; rodents, rabbits, cows and their relatives, and horses and their relatives are mammalian herbivores. Seed-eating is much more common than herbivory in birds. (Examples include parrots, pigeons, finches, and sparrows.) Major mammalian seed-eaters are squirrels, rats, and mice. Whereas vertebrate mutualists are beneficial for certain economically important plants, vertebrate herbivores and seed-eaters can cause millions of dollars of damage annually to many economically important crops. Humans, too, are vertebrates, and the interactions of plants and humans, especially through agriculture, has had profound consequences for each. SEE ALSO Coevolution; Pollination Biology.

Theodore H. Fleming

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Invasive Species

Plants that grow aggressively and outcompete other species are called invasive species. Invasive plants are usually those that were introduced, either intentionally or unintentionally, into a locality where they previously did not grow. Introduced plants, also called exotics or alien species, form an important part of our environment, contributing immensely to agriculture, horticulture, landscaping, and soil stabilization. But among the thousands of plant species introduced to North America, approximately 10 percent display the aggressive growth tendencies of invasive species. Although the terms *exotic*, *alien*, and *invasive* are sometimes used interchangeably, not all exotic plants are invasive. In addition, some native species, those plants that grew in an area prior to European settlement, can be invasive, especially as natural landscapes are altered.

Characteristics of Invasive Species

Invasive species are not a separate biological category, and all types of plants, including vines, trees, shrubs, ferns, and herbs, are represented by invasive species. They do, however, share certain characteristics that help them rapidly grow and invade new areas. Invasive plants typically exhibit at least some of the following:

- production of many seeds
- highly successful seed dispersal
- no special seed germination requirements
- grow in disturbed ground
- high photosynthetic rates
- thrive in high-nutrient conditions
- rapid growth and maturity
- early maturation
- reproduction by both seeds and vegetative means
- long flowering and fruiting periods

Most exotic plants do not pose an obvious threat to native plants when they are first introduced, but we do not fully understand the dynamics of what makes plants invasive. The same plant species can be invasive in one habitat or area and not aggressive in another. Sometimes many years separate the first introduction of a plant and its later spread as an invasive species. For example, Atlantic cord grass (*Spartina alterniflora*) was present in small areas on the Pacific coast for more than fifty years before it became invasive.

Often by the time a plant is recognized as being a major problem it has become so well established that eradication is difficult or impossible. Even when plants are recognized as a potential problem, finding the money and manpower needed to eliminate them may not be easy. For example, leafy spurge (*Euphorbia esula*), which forms dense stands that cattle refuse to graze, was seen as a potential problem in Ward County, North Dakota, in the 1950s. By the time funding was available to deal with the problem on both public and private lands, leafy spurge was present in all townships in the county and had increased from one small patch to about 12,000 acres.

Spread of Invasive Species

People have been the major factor in the spread of invasive species. Humans have always carried plants with them for food, medicine, fiber, ornament, or just curiosity. As human population has increased, so has the demand for food, housing, transportation, and other necessities of life. More and more land is disturbed to provide people with what they need and want, and disturbed land is where invasive species get their footholds. Increased international travel and global world trade also contribute to the problem. Invasive species have arrived in North America in the cargo holds of airplanes, as seeds in grain shipments, in the soil of ornamental plants, and as ship ballast. Improvements in transportation technology allow both people and plants to travel thousands of miles in just a few hours.

New environments provide an ideal place for invasive plants. These species leave behind the natural controls (usually insects) that kept them under control in their native habitats and can often spread unchecked. Some, such as the common dandelion (*Taraxacum officinale*), ox-eye daisy (*Chrysanthemum leucanthemum*) or tree-of-heaven (*Ailanthus altissima*), have become integrated over time into the flora of urban areas and are the dominant and familiar vegetation.

Most of the invasive species in North America are originally from Europe or Asia, areas with very similar climate. Many of these species were first introduced as ornamental plants. An excellent example is honeysuckle (*Lonicera* spp.), which was introduced in the late 1890s as horticultural shrubs and vines and for wildlife habitat improvement. Honeysuckle often outcompetes native plants due to earlier leaf expansion and later fall leaf retention. Large thickets of honeysuckle interfere with the life cycles of many native shrubs and herbs. These stands alter habitats by decreasing light and depleting soil moisture and nutrients. Some honeysuckle species also release chemicals into the soil that inhibit the growth of other plants. Fruits are consumed and passed by birds, which makes effective control difficult.

Another ornamental that turned invasive is kudzu (*Pueraria lobata*), a vine with attractive purple flowers that was first exhibited in the United States at the Philadelphia Centennial Exposition in 1876. It is now listed as a noxious weed in many states, especially in the South, where it smothers large trees as it clambers for light.

Accidental introduction is also a common way for invasive species to become established. Mile-a-minute weed (*Polygonum perfoliatum*), an Asian vine named for its fast growth rate, appeared in rhododendron nurseries in Pennsylvania in 1946, presumably the result of seeds mixed with imported plants. Since then it has spread to other areas in Pennsylvania as well as to surrounding states and is rapidly becoming a major problem along roadsides and other disturbed areas.

Purple loosestrife spreading in a wetland.

Impact and Eradication

The economic impact of invasive plants is staggering. They affect agriculture, the environment, and health. Invasive plants cause reductions in crop harvests as well as increased production costs. Farmers worldwide spend billions of dollars annually on chemicals and other methods to control weeds. The toll in human time is enormous, as hand-weeding of crops is the number one work task of 80 percent of people in the world. Some invasive species that contaminate harvested crops or pastures are toxic and pose a threat to both people and animals ingesting that food or milk.

Invasive plants are also a major threat to native plants and animals, including rare and endangered species. In fact, alien species are considered by some experts to be second only to habitat destruction as a threat to **biodiversity**. In the United States, for every acre of federal land destroyed by fire in 1995, two acres were lost to invasive plants. Two-thirds of all endangered species are impacted by invasive plants. Wetlands, home to many endangered plants, are especially susceptible to invasive species, such as purple loosestrife (*Lythrum salicaria*), which has taken over thousands of acres in at least forty-two states.

biodiversity degree of variety of life

The problem of invasive species affects all fifty states. Introduced species make up 8 to more than 50 percent of the total plant species of most states. Nowhere is the problem more serious than in Hawaii, where exotic species now outnumber native species. In Florida, at least 1.5 million acres of natural areas are infested with nonnative plants. Of mainland states, New York and Pennsylvania have the highest ratio of introduced-to-native species.

Methods for eradicating invasive plants range from hand-pulling to chemical controls. When weeding plants, it is important to disturb the soil as little as possible because disturbed areas are where invasive species can grow well. Other mechanical means include mulching soil to prevent or reduce seed germination, applying heat to seedlings, mowing, and girdling trees (pulling a strip of bark off all the way around the trunk to prevent the flow of nutrients). As more and more noxious weeds become resistant to chemical treatments, attempts at biocontrol (using natural predators) are

increasing. Researchers have identified thirteen different insect species that may potentially control leafy spurge, and a beetle that eats the leaves of purple loosestrife has already been released in some areas.

Perhaps most important is public awareness and participation in the problem. People should avoid using invasive plants in their yards and gardens. This can be a complicated task as some invasive species, such as purple loosestrife, are sold in garden stores and catalogs. Beware of any plants described as "spreading rapidly." Another important defense is being on the lookout for alien plants and removing them before they become a problem. Organized efforts at invasive plant removal are a major weapon in preventing their spread. In Utah, middle and high school students who participate in a Scotch Thistle Day each spring have significantly reduced the amount of this noxious weed in their area.

monoculture a large stand of a single crop species

colonize to inhabit a new area

Although most invasive species have been introduced from other areas of the world, native plants can become aggressive, especially as habitats are altered or destroyed. Boxelder (*Acer negundo*) and wild grapes (*Vitis* spp.) as well as other native species can form fairly exclusive **monocultures** that thrive in disturbed environments. On the other hand, some otherwise invasive species can be useful in heavily disturbed sites. For example, tree-of-heaven grows where other plants cannot, thus providing just the foothold needed by other species to **colonize**.

The problem of invasive species is a costly one in terms of time, money, and loss of native habitats and species. Since the 1950s, weed-associated losses and costs worldwide have increased exponentially and are continuing to spiral upward. Of the more than sixty-seven hundred plants worldwide that are considered to be invasive, only about two thousand presently occur in North America. This leaves more than four thousand invasive plants now growing in other countries that could in the future become a problem in the United States. SEE ALSO Endangered Species; Human Impacts; Kudzu; Seed Dispersal; Wetlands.

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Island Biogeography *See Biogeography.*

Jasmonates *See Senescence.*

K

Kudzu

Kudzu (*Pueraria lobata*, Fabaceae) is a woody vine whose extremely rapid and aggressive growth has made it a highly successful and widely disliked invasive species throughout much of the southern United States.

Kudzu overgrowing a forest in Georgia.

A native of Asia, kudzu was imported in the late 1800s as a shade-giving ornamental, and was widely planted in the 1930s to control erosion from cotton fields. In the mild and moist climate it prefers, and without its natural predators, kudzu spreads rapidly. In the United States, it covers more than three million acres across twenty-one southern states, blanketing an area nearly the size of Connecticut.

A kudzu vine can grow as much sixty feet in a growing season. It sets new roots at each **node**, thus forming a potential new plant every two or three feet. A five-acre field abandoned to kudzu may contain one hundred thousand plants, and the foliage may be two or more feet thick. The tap roots are massive, measuring up to seven inches across and six feet deep, and weighing up to two hundred pounds or more. Kudzu vines grow up and over almost anything, including trees, barns, and telephone wires. They can starve even full-grown trees of light, water, and nutrients.

node branching site on a stem

While kudzu has some nutritional value as livestock forage, it is too difficult to control to make it a valuable crop. Current eradication efforts use either repeated applications of herbicide or continuous, intensive grazing. SEE ALSO Fabaceae; Invasive Species.

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L

Landscape Architect

A landscape architect is an environmental design professional who applies the art and science of land planning and design on many scales, ranging from entire regions to cities, towns, neighborhoods, and residences. The profession is quite diverse, and students may attend more than sixty undergraduate and graduate programs in the United States and Canada, many of which offer comprehensive and/or individualized training in the following areas:

- **Landscape Design:** Outdoor space designing for residential, commercial, industrial, institutional, and public spaces
- **Site Planning:** Designing and arranging built and natural elements on the land
- **Urban/Town Planning:** Designing and planning layout and organization of urban areas, including urban design, and the development of public spaces such as plazas and streetscapes
- **Regional Landscape Planning:** Merging landscape architecture with environmental planning, including land and water resource management and environmental impact analysis
- **Park and Recreational Planning:** Creating or redesigning parks and recreational areas in cities, suburban and rural areas, and larger natural areas as part of national park, forest, and wildlife refuge systems

A landscape architect and his assistant work on a map in Raleigh, North Carolina.

- **Land Development Planning:** Working with real estate development projects, balancing the capability of the land to accommodate quality environments
- **Ecological Planning and Design:** Studying the interaction between people and the natural environment, focusing on flexibility for development, including highway design and planning
- **Historic Preservation and Reclamation:** Preserving, conserving, or restoring existing sites for ongoing and new use
- **Social and Behavioral Aspects of Landscape Design:** Designing for the special needs of the elderly or physically challenged

The study of plant sciences is often an integral part of the above specialties. Increased focus on ecological planning and natural systems design includes the study of native plant materials and **ecosystems**. The development of public and private gardens and recreation destinations places specific focus on ornamental horticulture using cultivated plant materials.

ecosystem an ecological community together with its environment

Opportunities abound for landscape architects working for residential and commercial real estate developers, federal and state agencies, city planning commissions, and individual property owners. Salaries vary widely depending on experience and whether one works for a private or public organization, but it equals or exceeds those of architects and civil engineers.

Future opportunities for landscape architects are extremely promising. The increasing complexity of projects requires interdisciplinary communication and commitment to improving the quality of life through the best design and management of places for people and other flora and fauna. SEE ALSO ARBORIST; HORTICULTURIST; ORNAMENTAL PLANTS.

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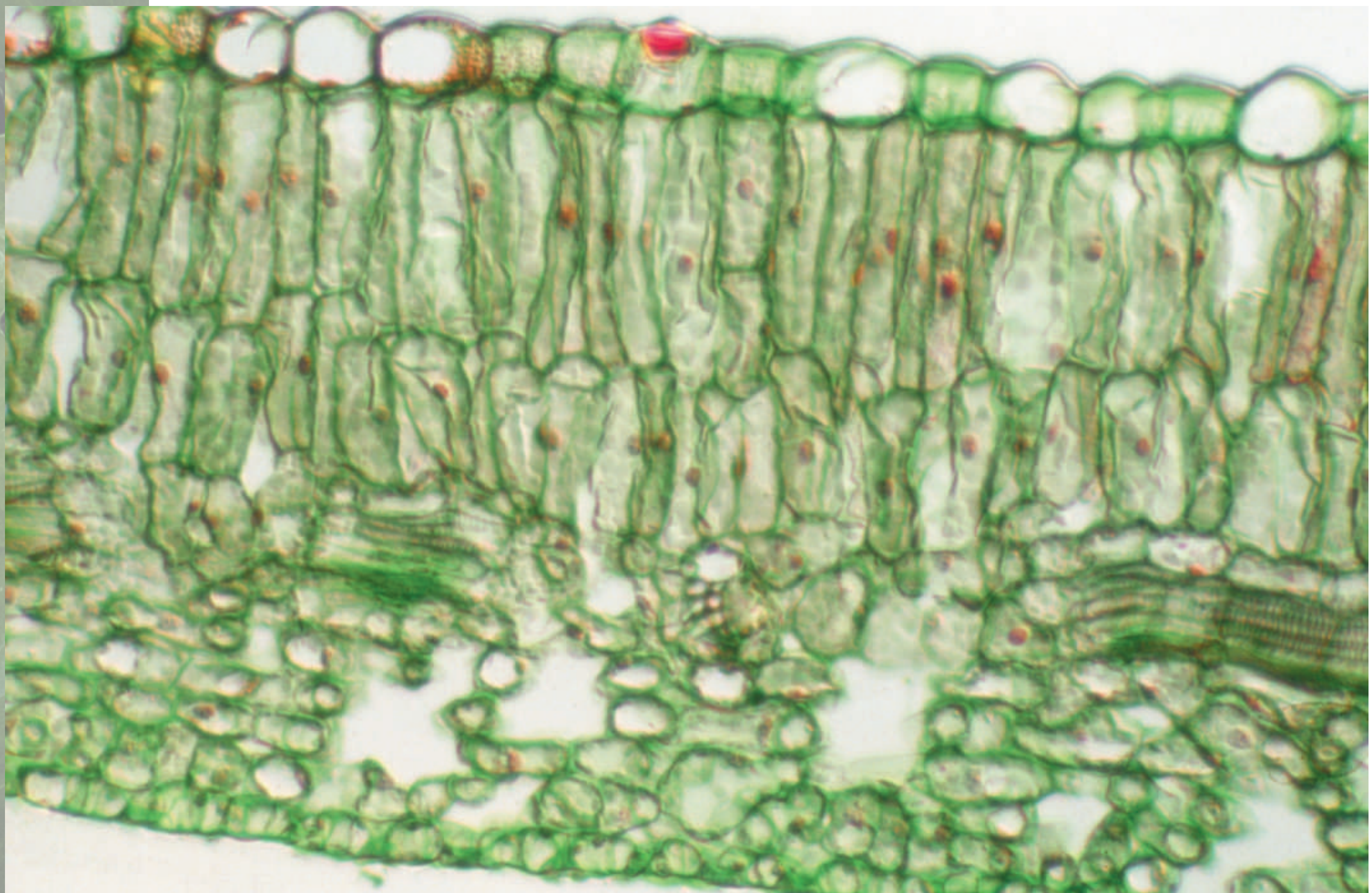
Leaves

Leaves are often the most conspicuous part of any plant. Leaves vary tremendously in shape and in size: from the tiny leaves (less than 1 millimeter across) of the floating aquatic plant duckweed to the giant leaves (more than 10 meters in length) of the raffia palm. Nevertheless, all leaves share certain features of construction and development and carry out the same basic function: photosynthesis.

Leaf Types

Leaves are designed to optimize the capture of light for photosynthesis. In dicots, leaves typically have a broad, flattened blade attached to a stalk or **petiole**. The flat shape of the blade facilitates the penetration of light

petiole the stalk of a leaf, by which it attaches to the stem



A micrograph of a transverse section of a leaf.

into the photosynthetic tissues within, while the petiole positions the blade so that it is shaded as little as possible by neighboring leaves. Leaf blades are referred to as simple when they are undivided and as compound when they are subdivided into individual leaflets. Compound leaves are either pinnately compound (like a rose leaf) or palmately compound (like a horse chestnut leaf). Simple leaves may also have complex shapes: In plants such as the maple or oak, leaves are highly lobed. The lobing of simple leaves and dissection of compound leaves are thought to serve the same function: The leaf maintains a large photosynthetic surface, but the complex outline allows the leaf to radiate heat energy to the surrounding atmosphere, thus maintaining photosynthetic tissues at optimum temperatures.

The leaves of monocots are designed along a different ground plan. The base of the leaf typically surrounds the stem, forming a leaf sheath. The leaf blade is borne at the tip of the sheath. In grasses, sedges, lilies, and orchids, the leaf blade is simple, long, and strap-shaped. In other monocots, such as palms, the blade is typically compound, and, like compound-leaved dicots, leaves may be pinnately compound (like a date palm) or palmately compound (like a fan palm). In palms and some other monocots, the junction of the sheath and blade forms a petiole-like structure.

Plant species are often recognized by their distinctive leaf shapes. Some species, however, are distinguished by producing more than one leaf shape on the same plant, a phenomenon known as heterophylly. Heteroblasty is the most common subtype of heterophylly and typifies plants such as ivy or eucalyptus, which produce one leaf shape early during the juvenile phase and another leaf shape later during the adult or reproductive stage. Another type of heteroblasty is environmentally induced heterophylly, in which specific environmental cues cause an immature leaf to develop along one of two or more alternate pathways. This type of heterophylly commonly results in the formation of sun and shade leaves on the same plant: Leaves that develop on the exposed edge of the canopy are narrow and thick, while those produced in the shaded interior are broad and thin.

Anatomy of Leaves

Despite tremendous variation in size and shape, leaves generally possess the same cell types and arrangement of internal tissues. Leaf veins form a transport system that extends throughout the leaf. Major veins are the large veins that can be seen with the naked eye. The xylem of major veins functions to import water and dissolved mineral nutrients from the rest of the plant to the leaf, while the phloem of major veins exports carbohydrates produced by leaf photosynthesis. The **vascular** tissues of major veins are associated with **collenchyma** and **sclerenchyma** tissues and so contribute to the support of the leaf. Smaller veins are called minor veins. They lack associated supporting tissue and are embedded in the ground photosynthetic tissue. Minor veins form a network that acts as a distribution system: They supply leaf cells with water and **solutes** from the xylem and load photosynthetic products into the phloem. Whether the arrangement of minor veins forms a netlike reticulate pattern (typical of dicots) or a gridlike pattern (typical of monocots), adjacent veins are usually no more than 200 micrometers apart. Thus water and solutes rarely have to diffuse more than 100 micrometers between vascular tissues and photosynthetic cells.

vascular related to transport of nutrients

collenchyma one of three plant cell types

sclerenchyma one of three plant cell types

solute a substance dissolved in a solution

The photosynthetic tissue of the leaf is called mesophyll. Mesophyll tissue contains **chloroplast**-packed cells of two distinct shapes: palisade **parenchyma** cells that are elongated and spongy parenchyma cells that are spherical or lobed. In leaves with a horizontal orientation, palisade cells form one or two layers toward the upper side of the leaf. Palisade parenchyma cells have dense chloroplasts and, in fact, capture most of the light energy penetrating the leaf. Up to 90 percent of total leaf photosynthesis may occur within palisade parenchyma cells. Spongy parenchyma cells are arrayed in several layers below the palisade. They are exposed to more diffused light and tend to have fewer chloroplasts. Both palisade and spongy parenchyma cells have a relatively high surface-to-volume ratio: this gives a large surface area for the diffusion of carbon dioxide from the intercellular air space of the leaf into the cell where photosynthesis takes place.

chloroplast the photosynthetic organelle of plants and algae

parenchyma one of three plant cell types

Cells of the leaf **epidermis** typically are shaped like jigsaw puzzle pieces, which is thought to lend structural support to the leaf blade. **Stomata** usually occur on both the upper and lower surfaces of the leaf. The thinness of most leaf blades ensures that carbon dioxide diffusing inward through the stomatal pores will rapidly reach the mesophyll cells. While leaves are designed to maximize the uptake of CO_2 through the stomatal pores, they lose water vapor through those same pores while the stomates are open. Some plant species reduce such water loss by restricting the stomates to the lower, shaded side of the leaf blade where temperatures are lower and the diffusive loss of water vapor is slower.

epidermis outer layer of cells

stomata openings between guard cells on the underside of leaves that allow gas exchange

Development of Leaves

apical meristem the growing tip of a plant

primordium the earliest and most primitive form of a leaf

Leaves are formed on the flanks of the shoot **apical meristem**. Leaf formation involves four overlapping stages: leaf initiation, morphogenesis, histogenesis, and expansion. Initiation occurs when an alteration of growth pattern within the shoot apical meristem results in a definite protuberance on the surface of the meristem, the leaf **primordium.** The leaf primordium is produced in a precise location on the meristem according to the phyllotaxis (leaf arrangement) of that particular species. In most dicots, leaf arrangement is helical, and each new leaf primordium is produced in the location that will continue the helix, 137.5 degrees from the last formed leaf. In most monocots, leaf arrangement is distichous, meaning each new leaf primordium is produced at 180 degrees from the previous leaf.

Morphogenesis is the development of the leaf's shape. In dicots, the primordium grows perpendicular to the meristem to form a fingerlike projection. Once the projection is formed, the primordium alters its growth direction to form a ledge around the margin of the protuberance. This ledge becomes the leaf blade, while the thicker original protuberance forms the petiole-midrib axis. At this stage of development, the distribution of growth is diffused, with the whole blade and petiole-midrib axis growing at an even rate. In species with a complex leaf shape, such as a lobed or compound blade, the distribution of growth becomes uneven: growth is enhanced where a lobe or a leaflet will be formed and suppressed between the lobes or leaflets. These events occur very early, so that a leaf often displays its mature shape when it is less than 1 millimeter in length.

In monocots, the original leaf primordium is formed in the same way, but its pattern of growth differs almost from the start. The zone of leaf initiation extends around the flanks of the shoot apical meristem, giving a crescent-shaped primordium. The crescent-shaped primordium then grows vertically. The "wrap-around" base becomes the leaf sheath, and the apical end becomes the strap-shaped blade. Monocots with more complex leaf shapes, such as palms, have a highly specialized pattern of morphogenesis.

Histogenesis is the process of tissue development. While the leaf is expanding and acquiring its final shape, precursor cells of all the tissue systems are undergoing cell proliferation. Cell proliferation is at first distributed throughout the leaf, but as expansion continues, cell division gradually ceases beginning near the tip of the leaf until it finally becomes restricted to the leaf base. In most dicots, this period is brief: the full complement of leaf cells may be already present when the leaf is only 10 percent of its final size.

intercalary inserted; between

In many monocots, cells near the base of the leaf continue to divide throughout the life of the leaf, forming an **intercalary** meristem. When you cut the grass of your lawn, cells in the intercalary meristem are induced to divide, producing more leaf tissue toward the leaf tip.

As leaf cells cease dividing, they first enlarge and then complete differentiation, acquiring the distinctive characteristics of specialized cell types. As with cell proliferation, cell differentiation occurs in a tip-to-base, or basipetal, direction.

Leaf expansion overlaps the morphogenesis and histogenesis stages. Usually all parts of the leaf expand the same amount so that the shape of the young leaf is preserved at maturity; this pattern is called isometric growth. In some species, however, different parts of the leaf expand at different rates, called allometric growth. Allometric growth can either enhance or minimize the degree of lobing in a leaf: if the lobes grow more than the interlobe region (the sinus), they will become more pronounced. In contrast, a leaf such as that of the nasturtium actually starts out with a lobed shape but becomes smooth and round in outline through increased growth of the sinus.

Detail of a cabbage leaf.

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

Leaf Modifications

Although leaves tend to share the same ground plan, species that have adapted to extreme environmental conditions often have highly modified leaves. Two well-known examples are the leaves of xerophytes, plants adapted to arid environments, and leaves of hydrophytes, plants adapted to wet environments. Xerophytes are desert plants that must carry out photosynthesis and conserve water at the same time. Xerophytes reduce water loss by having small, but thick, leaves, thus reducing the surface area for evaporative water loss. Light intensity is usually high in the desert, so sufficient light penetrates to all photosynthetic mesophyll cells, even in a thick leaf. Xerophytes have a thick **cuticle** and waxes on the leaf surface, further reducing water loss. Their leaves often have a thick covering of trichomes that both trap a layer of moister air next to the leaf and reflect heat energy away from photosynthetic tissues. Some xerophytes, such as the oleander, have their stomates restricted to pits called stomatal crypts that further reduce evaporation of water vapor. A few specialized desert plants such as the clock plant hold their leaf blades parallel to the sun's rays throughout the day, using a specialized region of the leaf petiole called a pulvinus. The leaf photosynthetic tissue is exposed to sufficient light but absorbs less heat energy, thus keeping internal tissue temperatures cooler.

Hydrophytes face the opposite challenge to xerophytes. Their leaves are submerged, so there is no shortage of water, but they must photosynthesize under conditions of low light and low availability of carbon dioxide. Hydrophyte leaves are typically very thin, both to absorb the low, diffused light available underwater and to allow for the diffusion of dissolved carbon dioxide and minerals into leaf tissue. Hydrophytes lack stomata and have only a thin cuticle. They also have reduced vascular tissue. (Xylem is missing altogether in the leaves of some hydrophytes.) As hydrophyte leaves are buoyed by water, there is little need for supporting sclerenchyma tissue.

Many other examples of highly modified leaves occur as specialized adaptations among the flowering plants. Insectivorous plants have leaves that serve as traps for their insect prey. Cacti and many other desert plants have leaves that are modified as spines that serve to protect the plant from herbivores while the stems carry out photosynthesis. Some monocots have leaves modified for storage: the leaf sheaths of an onion bulb are thickened, and the mesophyll parenchyma cells are filled with stored sugars.

Evolution of Leaves

The fossil record shows that the first land plants lacked leaves—or rather the stem functioned in both photosynthesis and support. Only toward the end of the Devonian period, about 350 million years ago, did plants begin to bear distinct leaves borne on stems. Leaves of some of these early land plants were huge. Tree club mosses and primitive conifers called Cordaites had meter-long strap-shaped leaves where their modern relatives have highly reduced scale or needle leaves. Fossils of some of the earliest flowering plants from the beginning of the Cretaceous period, about 125 million years ago, show that leaves were of medium size and simple in shape. During the evolutionary diversification of the flowering plants, some groups have developed large, highly elaborate leaves, while others form small, reduced leaves. The early evolutionary divergence of the dicot and monocot lines is reflected in the different basic construction and mode of development of leaves in these two groups. SEE ALSO Anatomy of Plants; Aquatic Plants; Cacti; Carnivorous Plants; Photosynthesis, Carbon Fixation and; Photosynthesis, Light Reactions and; Phyllotaxis; Tissues; Trichomes.

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Leguminosae *See Fabaceae.*

Lichens

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

Lichens are the "dynamic duo" of the plant world. They consist of a fungus and a photosynthetic partner (green algae or **cyanobacteria**, or sometimes both) that live and grow so intimately interconnected that they appear to be a single organism. The fungus surrounds its green partner and shares in the sugars and other carbohydrates that the alga or cyanobacterium produces by photosynthesis. At the same time the fungus provides a protected environment for its food-producing partner and expands its potential habitats. Lichen fungi have a range of nutritional relationships with their associated algae or cyanobacteria from almost pure parasitism to a very benign association called symbiosis, or, more specifically, mutualistic symbiosis, wherein both partners benefit equally from the partnership. Lichens are an extremely successful life form, with thousands of species throughout the world. Some are extremely tiny and inconspicuous, little more than a black or gray smudge, but others can form broad, brightly colored patches or grow to be up to 3 meters long.

Fungal and Algal Components of Lichens

The fungi that form lichens mainly belong to the sac fungi or Ascomycetes, although a few are mushroom-forming fungi, the Basidiomycetes. Each recognizable lichen (with a few interesting exceptions) represents a separate species of fungus; about fourteen thousand are known. The name

The curly edged frondose (foliose) lichen *Parmelia caperata* in Taynish Woods in Scotland.

we give to each lichen is actually the name of its fungal component. There are, however, only a few hundred species of photosynthetic **symbionts** (photobionts for short) that are involved in lichen partnerships. Lichen fungi are very choosy about their photobionts, and so each recognizable lichen generally contains a specific photobiont. Any given photobiont may, however, be found in many different lichens. A number of lichens associate with a green alga as their main photosynthetic partner but also produce small warts or gall-like bumps containing cyanobacteria, which contribute to the lichen's nutrition and survival.

symbiont one member of a symbiotic association

Lichen Types and Reproduction

Lichens come in many shapes and sizes. They can be roughly grouped into four growth types: crustose, foliose, squamulose, and fruticose. Crustose lichens form a thin or thick crust so tightly attached to the material on which it grows (the substrate) that one has to remove the substrate together with the lichen to make a collection. A foliose lichen is leaflike; it is flat and has a clearly distinguishable upper and lower surface. Foliose lichens are attached to the substrate directly by the lower surface or by means of tiny hairlike structures called rhizines. Squamulose lichens are scalelike with flat lobes as in foliose lichens but more like crustose lichens in size and stature. Fruticose lichens are clearly three dimensional, growing vertically as stalks or shrubby cushions or hanging down from branches or rock faces with hair- or strap-shaped branches.

medulla middle part

The arrangement of tissues within most lichens follows the same basic plan. In a typical foliose lichen, a relatively tough upper cortex functions as a protective layer. Below the cortex is a green layer formed by the photobiont, then comes a cottony **medulla**, and, finally, on the lower surface, there is usually a protective lower cortex. The rhizines develop from the lower cortex.

Lichen reproduction is rather complex because at least two organisms are involved. The lichen fungus can produce sexual fruiting bodies and spores, but the photobionts reproduce only by cell division within the lichen. When a fungal spore is dispersed by wind or water, it can germinate almost anywhere, but it will form a new lichen only if it encounters the right kind of photobiont. This is a chancy business, and the vast majority of spores perish without forming new lichens.

There is, however, a less perilous way for lichens to reproduce. Any fragment of a lichen containing both the fungus and photobiont has the potential of developing into a new lichen. Many lichens have, in fact, evolved special, easily dispersed fragments in the form of powdery particles (soredia) or spherical to elongated granules or outgrowths (isidia).

Ecology of Lichens

Although lichens as a whole can be found growing on a wide variety of surfaces including rock, bark, wood, leaves, peat, and soil, individual species are more or less confined to specific substrates. Lichens are most conspicuous where other forms of vegetation are sparse, such as the bark of roadside trees or the surface of granitic boulders. They are usually the first organisms to invade entirely bare rock, contributing to the first particles of soil on the rock surface. Lichens carpet the ground in the vast boreal forests of the north, drape the trees and shrubs of foggy coastal regions and tropical cloud forests, and cover the exposed rocks on mountaintops and in the Arctic. They occur from the tropics to the polar regions and from lake edges and seashores to the desert. In general, however, lichens do best where there is much light, moist air, and cool temperatures. Lichens are notoriously sensitive to even small amounts of air pollution, especially the sulfur dioxide so common in cities and near factories, and large cities often have no lichens at all. Their disappearance from an area is an early sign of deteriorating air quality.

Importance and Economic Uses of Lichens

ecosystem an ecological community together with its environment

The importance of lichens to the natural world and to humans is not well appreciated except, perhaps, for their role in soil formation. Lichens containing cyanobacteria are important sources of nitrogen in certain forest and desert **ecosystems**. The ground-dwelling boreal lichens preserve the ground's moisture. Lichens growing in the dry soils of the interior prairies and foothills prevent erosion.

Although lichens have usually been used as human food only in times of emergency (they are unpalatable and have very little nutritional value), a few lichen delicacies are enjoyed by native people of western North America and by the Japanese. Reindeer lichens in the boreal forest, however, are essential as winter forage for caribou herds, which are, in turn, basic to the survival and culture of northern native people. Some lichens yield a chemical called usnic acid, which is an effective antibiotic against certain types of bacteria. Other chemicals produced only by lichens have been used as a source of rusty red, yellow, and purple dyes for coloring wool and silk. Extracts of oakmoss lichens have been used for generations in the perfume industry. The litmus used to determine the acidity of solutions comes from a lichen. The most important use of lichens today, however, is for detecting and monitoring air pollution. SEE ALSO Algae; Boreal Forest; Fungi; Plant Community Processes.

Irwin M. Brodo

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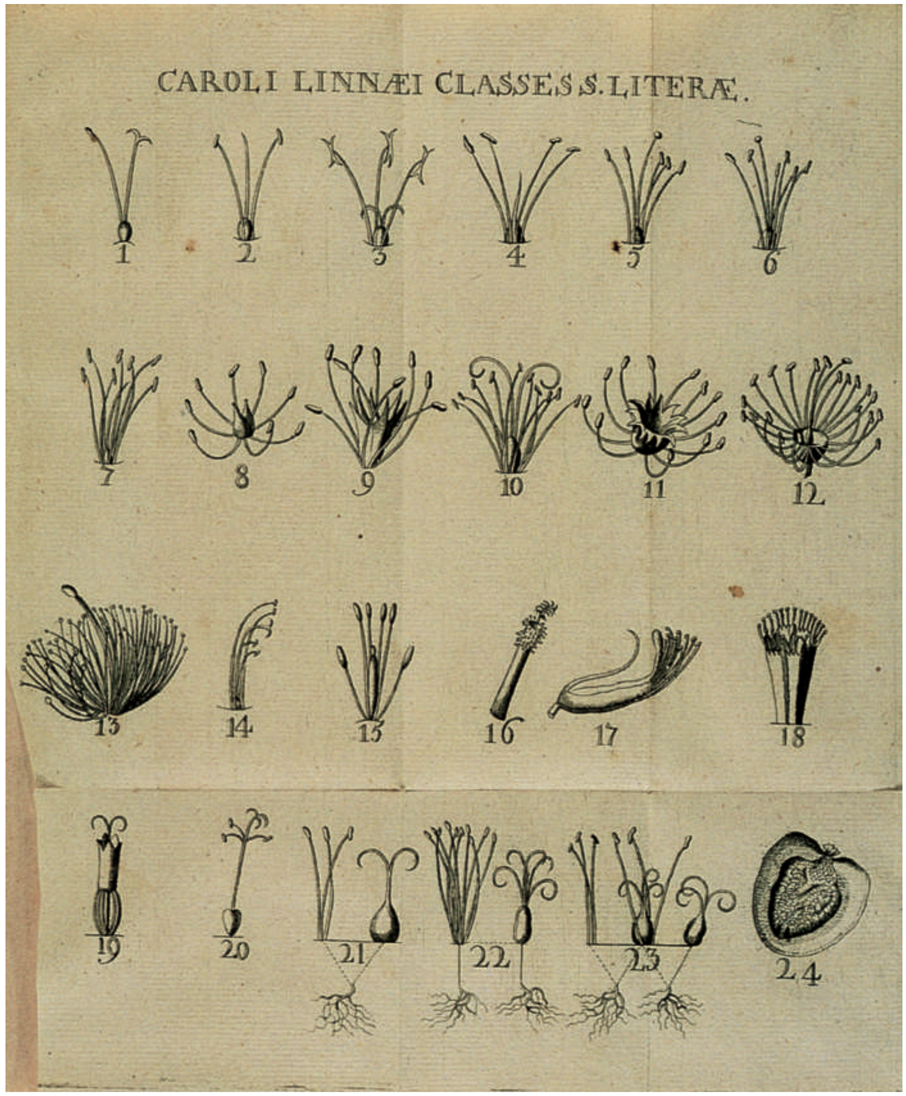
Linnaeus, Carolus

Swedish Botanist
1707–1778

Carolus Linnaeus.

Swedish botanist Carolus Linnaeus is best remembered for his classification system and binomial system of nomenclature. He brought order to the chaotic state of biological knowledge in the eighteenth century, introducing a systematic means of processing and organizing information on plants and animals. His particular interest was in plants, especially flowering plants, and the bulk of his efforts and publications focused on botanical studies. His most lasting contribution to biology is his binomial nomenclatural system, which grew out of what was for him a more primary focus: the development of a comprehensive system for classifying plants and animals.

Also known as Carl Linnaeus or Carl von Linné, he was born in Småland, Sweden, and even in his early years displayed an unusual interest in plants. His father, a curate in the Lutheran church, taught him many plant names. In adolescence Linnaeus learned about the doctrine of sexual reproduction in plants, which at that time was still a relatively recent concept. While still a medical student at universities in Lund and Uppsala, he began to develop a classification system based on the reproductive organs of plants. Faculty recognized his abilities and asked him to conduct lectures on botany. In 1732 he received support from the Swedish Royal Academy of Science



A plate from Linnaeus's 1737 work *Genera Plantarum* showing the twenty-four classes of Linnaeus's sexual system.

to travel to Lapland to observe the plants and animals there and how people lived and supported themselves. This trip made a lasting impression on young Linnaeus. He wrote about the plants he observed in *Flora Lapponica* (1737), and the **specimens** he collected in Lapland are now at the Institut de France, Paris.

specimen object or organism under consideration

In 1735 Linnaeus traveled to Holland to get a medical degree at Harderwijk. While in Holland he met prominent naturalists and was able to publish some of his own research. He made short trips to England, Germany, and France, again meeting important naturalists. In Holland he worked for George Clifford, a wealthy merchant with an extensive private botanical garden, which Linnaeus worked on and catalogued. This opportunity exposed Linnaeus to a wide range of plants that he would not have seen in his native Sweden, an experience that aided him in developing his ideas about classification. A catalogue of plants in Clifford's garden was published as *Hortus Cliffortianus* (1738).

Among the ten manuscripts Linnaeus published while in Holland were *Systema Naturae* (1735) and *Genera Plantarum* (1737). The former contained the first appearance of his classification scheme, while the latter contained his natural definitions of **genera**, building on work previously done by Joseph Pitton de Tournefort (1656–1708) and others.

genera plural of genus; a taxonomic level above species

Linnaeus returned to Sweden in 1738, was married, and practiced medicine in Stockholm for three years. In 1741 he was appointed a professor at the university in Uppsala, where he remained for the rest of his life, teaching, collecting and studying plants, and publishing. He was popular with his students and trained among them many enthusiastic naturalists. Early in his university career he traveled around Sweden, but after 1749 he stayed in Uppsala, sending a number of his students out on plant exploration journeys to many parts of the world. His landmark *Species Plantarum* (1753) and many other publications trace the development of his thought through the course of his career.

Linnaeus received many honors during his lifetime and was famous in Sweden and abroad for his ideas about classification and nomenclature. The eighteenth century was marked by a collective desire to gather and organize the whole of knowledge in encyclopedic schemes, and certainly Linnaeus's efforts were in harmony with the spirit of his times. His unusual talents for systematic organization and for **intuiting** the relationships among plants allowed him to accomplish a methodical review and theoretical organization of the natural world on a massive scale at a time when such work was desperately needed. His precise terminology, use of an international language, and global scope ensured widespread applicability and usability of his system. Modern systematic biology began with his mid-eighteenth-century publications. Historians of science recognize this by referring to earlier publications in the life sciences as "pre-Linnaean literature." Linnaeus's main collections are held by the Linnean Society of London, and other collections that he made throughout his lifetime are scattered at various institutions.

intuiting using intuition

Classification of Organisms

Naturalists in eighteenth-century Europe were faced with a bewildering and ever-growing number of previously unencountered plants and animals, the result of European voyages of exploration. Many sought to develop some sort of natural classification system that would organize plants and animals according to the true relationships among things in the natural world. Such a system would necessarily be based on a complex assessment of numerous characteristics of the things being classified. This goal proved very difficult to attain, and some began to devise more artificial systems, sacrificing a broad focus on natural affinities for an easier-to-apply method using one or a few characteristics by which to sort and organize living organisms.

Linnaeus too saw the desirability of a natural system, and he published some basic principles for attaining one, but there were still not enough plants and animals known to allow for a sufficiently broad synthesis. Thus, for plants, he worked out an extremely simple system based on counting stamens and **pistils**, which provided an easy, practical, and usable means for sorting and identifying plants. The scheme was first published in *Systema Naturae* (1735), which contained tables in which the "three kingdoms of nature"—animal, vegetable, and mineral—were comprehensively classified.

pistil the female reproductive organ

For plants Linnaeus defined a genus (plural: genera) as a group of species with similar flowers and fruits. Genera were grouped into twenty-three classes of flowering plants by the number and disposition of stamens, with a twenty-fourth class for apparently nonflowering plants. Within classes they were arranged into smaller groups or orders according to the number and disposition of pistils. This scheme was called the "sexual system" because of its focus on the reproductive organs of plants. It was simple enough that even amateurs could use it to sort plants and ascertain whether they were already known to science.

The eighteenth century saw an information explosion in the natural sciences, and the utility and practicality of Linnaeus's classification scheme lay in the way it facilitated processing of information about the natural world. His sexual system of classification, although controversial and not widely accepted at first, was in general use in many countries for nearly a century, after which it was supplanted by more natural systems. Although it fell from use, in its time it reduced confusion in the study of organisms and facilitated the advancement of botany and zoology by providing a stopgap measure until a natural classification system could be developed.

Naming of Organisms

nomenclatural related to naming or naming conventions

polynomial "many-named"; a name composed of several parts

The **nomenclatural** system that Linnaeus developed in the process of classifying nature proved to be of greater and more lasting benefit to biological science. In the century before Linnaeus, plants and animals were given long, descriptive names (known as **polynomials**) to differentiate them. For example, the polynomial name of catnip was "Nepeta floribus interrupte spicatus penduncculatis" (Nepeta with flowers in an interrupted pedunculated spike). There were no universally applied rules for constructing these names, however, resulting in considerable confusion in naming and referring to living things.

Linnaeus's solution to this problem, which was first applied to the plant world, was to group plants by genus and provide genus names (retaining many already in familiar use, or coining new ones), and then to give each species within a genus a "trivial" name, or what is known now as a specific epithet, so that each would have a unique two-part name, thereby unequivocally identifying that species. These trivial names, often in the form of Latin adjectives, were not necessarily descriptive, but they were linked to descriptive information, diagnoses, and references to previous descriptions in botanical literature. For example, he named catnip *Nepeta cataria* (cat-associated Nepeta). This enabled scientists to identify organisms with greater certainty, and provided a solid means for expanding and advancing knowledge. All in all, Linnaeus named approximately forty-four hundred species of animals and seventy-seven hundred species of plants.

The use of shorter names did not originate with Linnaeus. Folk names for plants and animals are typically short, and some scientists, notably Caspar Bauhin (1560–1624), used one- or two-word names when possible. However, pre-Linnaean names were often longer, using more adjectives in order to differentiate species within genera. Linnaeus was the first to construct a methodical and consistent nomenclatural system and to apply it to all living organisms then known to European science. His system was so comprehensive and so conducive to an integrated view of past and contemporary botanical studies that it won widespread acceptance and continues in current usage.

The nomenclatural system for plants was first published in his landmark work, *Species Plantarum* (1753). For animals, a similar system was published in the tenth edition of *Systema Naturae* (1758). These two works form the baseline for current nomenclatural practice in botany and zoology. Taxonomists in both disciplines still refer to Linnaeus's works when checking names of organisms, as mandated by international codes of nomenclature in both disciplines. SEE ALSO HERBARIA; TAXONOMIST; TAXONOMY; TAXONOMY, HISTORY OF.

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Lipids

Lipids are a group of **compounds** that are rich in carbon-hydrogen bonds and are generally insoluble in water. The main categories are glycerolipids, sterols, and waxes.

compound a substance formed from two or more elements

Glycerolipids have fatty acids attached to one or more of the three carbons of glycerol. If three fatty acids are attached, the molecule is triacylglycerol, which is a primary storage form of carbon and energy in plants. Triacylglycerol is concentrated in many seeds for use during germination, and so seeds are of commercial importance as sources of fats and oils for cooking and industry. Diacylglycerol (DAG), which has two fatty acids, plays a role in cell signaling. Glycerolipids without any attached charged groups are known as neutral lipids.

If a polar molecule is added as a headgroup to DAG, the complex becomes a polar glycerolipid. The most common are phospholipids, the primary lipid component of higher plant membranes outside the plastids. Phospholipids are named after the headgroup, so if choline is present along with phosphate, the lipid is phosphatidylcholine. Several other headgroups exist. Polar lipids without phosphate also are important membrane molecules; for example, digalactosyldiacylglycerol, with two sugars as a headgroup, is a major component of **chloroplast** membranes.

chloroplast the photosynthetic organelle of plants and algae

Sterols are complex ring structures that are also major components of membranes. Some, such as brassinosteroids, also serve hormonal functions.

Waxes are elongated and modified fatty acids. They are found on the surfaces of plants, are highly impervious to water, and play a protective role. SEE ALSO ANATOMY OF PLANTS; HORMONES; OILS, PLANT-DERIVED.

Thomas S. Moore

Lycopods *See Seedless Vascular Plants.*

M

Maize *See Corn.*

McClintock, Barbara

American Botanical Geneticist
1902–1992

Barbara McClintock.

Barbara McClintock, a pioneering botanical geneticist, was awarded the Nobel Prize in physiology or medicine in 1983 for her investigations on transposable genetic elements. She was born on June 16, 1902, in Hartford, Connecticut, and with her family soon moved to Brooklyn, New York, where she attended public schools. After graduating high school at age sixteen, McClintock attended the New York State College of Agriculture at Cornell, where she excelled in the field of plant genetics and graduated, in 1923, with a Bachelor of Science (B.S.) in Agriculture, having concentrated in plant breeding and botany.

Career at Cornell

Awarded Cornell's graduate scholarship in botany for 1923–24, which supported her during the first year of her graduate studies, McClintock concentrated on **cytology,** genetics, and zoology. She received her master's degree (A.M.) in 1925 and a doctoral degree (Ph.D.) in 1927. Her master's thesis was a literature review of cytological investigations in cereals, with particular attention paid to wheat. In the summer of 1925, as a research assistant in botany, she discovered a corn plant that had three complete sets of chromosomes (a triploid). Then she independently applied a new technique for studying the chromosomes in the pollen of this plant and published these findings the following year. McClintock investigated the cytology and genetics of this unusual triploid plant for her dissertation.

cytology the microscopic study of cells

Upon completing her doctorate in June 1927, McClintock became an instructor at Cornell and continued to pursue her studies on the triploid corn plant and its offspring. When triploid plants are crossed to plants with two normal sets of chromosomes, called diploids, they can produce offspring known as trisomics. Trisomics have a diploid set of chromosomes plus one extra chromosome. Plants with extra chromomes could be used for correlating genes with their chromosomes if one could distinguish the extra chromosome in the microscope. McClintock's continued investigations on the chromosomes of corn led her to devise a technique for distinguishing the plants' ten individual chromosomes.

In 1929, in the journal *Science*, McClintock published the first description of the chromosomes in corn. She knew that having the ability to recognize each chromosome individually would now permit researchers to identify genes with their chromosomes. Using a technique of observing genetic ratios in her trisomic plants and comparing the ratios with plants having extra chromosomes, McClintock cooperated with and guided graduate students to determine the location of many genes grouped together (linkage groups) on six of the ten chromosomes in corn.

Around the same time McClintock devised a way to cytologically observe pieces of one chromosome attached to another chromosome. These translocation or interchange chromosomes stained darkly in the microscope and could be easily observed during cell division (meiosis) to produce pollen grains. The interchange chromosomes were then used to locate the remaining four linkage groups with their chromosomes. They were also used to explain how some corn plants become **sterile**. In 1931 McClintock guided graduate student Harriet Creighton in demonstrating cytological "crossing over," in which chromosomes break and recombine to create genetic changes. It was the first cytological proof that demonstrated the genetic theory that linked genes on paired chromosomes (homologues) did exchange places from one paired chromosome to another. It confirmed the chromosomal theory of inheritance for which Thomas Hunt Morgan would be awarded a Nobel prize in 1933.

sterile unable to reproduce

McClintock hoped for a research appointment commensurate with her qualifications. By 1931, however, the country was suffering from the Great Depression and research jobs at universities were not abundant, particularly for women. However, because of McClintock's excellent work and reputation, in 1931 she was awarded a National Research Council (NRC) fellowship to perform research with two leading corn geneticists, Ernest Gustof Anderson at the California Insititute of Technology (Caltech) and Lewis Stadler of the University of Missouri. Stadler, who was studying the physical changes (mutations) in plants caused by X rays, invited McClintock to study the chromosomes of his irridiated plants. She discovered that observable changes in the plant were due to missing pieces of chromosomes in the cell. At Caltech she employed interchange chromosomes to investigate the **nucleolar** organizer region in cells.

nucleolar related to the nucleolus

After a short period in Germany in 1933 studying on a Guggenheim fellowship, McClintock returned to Cornell, where she continued her research of the cytology of X-rayed plants that she had first examined at Missouri. This research led her to clarify and explain how some chromosomes became ring shaped, were lost during cell replication, or resulted in physical differences in plant tissues. These investigations led to her studies of the breakage-fusion-bridge cycle in corn chromosomes and would eventually lead, in 1950, to her revolutionary proposal that genes on chromosomes moved (transposed) from one place to another on the same chromosome and that they could also move to different chromosomes.

Career at Cold Spring Harbor

In 1936 McClintock, at Stadler's urging, accepted a genetics research and teaching position at the University of Missouri, which she held for five years, until she seized an opportunity to be a visiting professor at Columbia University and a visiting investigator in the genetics department of the Carnegie Institution of Washington (CIW), working at Cold Spring Harbor on Long Island in New York. She was offered a permanent job at Cold Spring Harbor in 1943 and spent the rest of her life working there with brief visiting professor appointments at Stanford University, Caltech, and Cornell.

In the winter of 1944 McClintock was invited by a former Cornell colleague, George Beadle, to go to Stanford to study the chromosomes of the pink bread mold *Neurospora*. Within ten weeks she was able to describe the fungal chromosomes and demonstrate their movement during cell division. This work was important to an understanding of the life history of the organism, and the fungus would be employed by Beadle and his colleagues to illucidate how genes control cell metablolism. In 1958 Beadle shared a Nobel Prize for that work.

Returning to Cold Spring Harbor in 1945, McClintock traced genes through the changes in colored kernels of corn. In that same year she was elected president of the Genetics Society of America. Over the next few years, using genetic and cytological experiments in the corn plant (*Zea mays*), she concluded that genetic elements (transposable elements, or transposons) can move from place to place in the **genome** and may control expression of other genes (hence called controlling elements). She published her findings in the 1950s, and more than thirty years later, in 1983, she was honored with the Nobel Prize for her remarkable discovery.

genome the genetic material of an organism

Many have wondered why it took so long for McClintock's work in transposition to be recognized by the leaders in the scientific community. One reason could be that although she studied corn chromosomes employing cytogenetic techniques, other researchers studied simpler organisms (bacteria and their viruses) and used molecular techniques. McClintock's experiments were complex and laborious, taking months or even years to yield results. Molecular studies in simpler organisms gave almost immediate answers, thus providing their researchers with instant celebrity. Additionally, McClintock's findings contradicted the prevailing view that all genes were permanently in a linear sequence on chromosomes.

Further, although McClintock's conclusion that genes could move from place to place in the corn genome was accepted, the idea was considered peculiar to corn, probably not universally relevant to all organisms. It was not until the 1970s when transposons were found in a number of other organisms, first in bacteria and then in most organisms studied by geneticists, that the value of McClintock's initial studies realized. Research on transposable elements, or transposons, led to the revolution in modern recombinant deoxyribonucleic acid (DNA) technology that has played a significant role in medicine and agriculture. When McClintock's work was rediscovered, she was recognized and rewarded with the Nobel Prize for her great insights. McClintock died on September 2, 1992, in Huntington on Long Island, New York. SEE ALSO CHROMOSOMES; GENETIC MECHANISMS AND DEVELOPMENT; POLYPLOIDY.

Lee B. Kass

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Medicinal Plants

Plants can not run away from their enemies nor get rid of troublesome pests as humans or other animals do, so what have they evolved to protect themselves? Whatever this protection is it must be successful, for the diversity and richness of green plants is extraordinary, and their dominance in most **ecosystems** of the world is unquestioned. Plant successes are closely intertwined with the evolution and production of highly diverse **compounds** known as secondary metabolites, compounds that are not essential for growth and reproduction, but rather, through interaction with their environment, enhance plant prospects of survival. These metabolites are therefore plant agents for chemical warfare, allowing plants to ward off microorganisms, insects, and other animals acting as predators and **pathogens**. Such compounds may also be valuable to humans for the same purposes, and therefore may be used as medicines.

ecosystem an ecological community together with its environment

compound a substance formed from two or more elements

pathogen disease-causing organism

What Characterizes Medicinal Plants

There are twenty thousand known secondary plant metabolites, all exhibiting a remarkable array of organic compounds that clearly provide a selective advantage to the producer, which outweighs their cost of production. Humans benefit from their production by using many of them for medicinal purposes to fight infections and diseases. An estimated two-fifths of all modern pharmaceutical products in the United States contain one or more naturally derived ingredients, the majority of which are secondary metabolites, such as alkaloids, glycosides, terpenes, steroids, and other classes grouped according to their physiological activity in humans or chemical structure. To illustrate the breadth of human reliance on medicinal plants, the accompanying table provides a list of the most significant plants, their uses in modern medicine, and the major secondary metabolites responsible for their activities. This list grows annually as new plants are found with desired activities and remedies to become pharmaceuticals for use in medicine.

COMMON MEDICINAL PLANTS AND THEIR USES

Scientific Name	Common Name	Family	Compounds	Compound Class	Uses
Atropa belladonna, Duboisia myoporoides	Belladonna	Solanaceae	Atropine, scopolamine	Alkaloid	Anticholinergic, motion sickness, mydriatic
Cassia/Senna species	Senna	Fabaceae	Sennoside	Glycoside, anthraquinone	Laxative
Catharanthus roseus	Madagascar periwinkle	Apocynaceae	Vincristine, vinblastine	Alkaloid	Anticancer (antileukemia)
Chondrodendron tomentosa, Curarea toxicofera	Curare	Menispermaceae	(+)–Tubocurarine	Alkaloid	Reversible muscle relaxant
Cinchona calisaya, Cinchona officinalis	Jesuits' bark	Rubiaceae	Quinine, quinidine	Alkaloid	Antimalaria (quinine), antiarrhythmia (quinidine)
Colchicum autumnale	Autumn crocus	Liliaceae	Colchicine	Alkaloid	Gout
Digitalis lanata, Digitalis purpurea	Foxglove	Scrophulariaceae	Digoxin, digitoxin, lanatosides	Cardiac glycoside (steroidal)	Heart failure and irregularity
Dioscorea species	Yam	Dioscoreaceae	Diosgenin, precursor of human hormones and cortisone	Saponin glycoside (steroidal)	Female oral contraceptives, topical creams
Ephedra sinica	Ephedra, Ma huang	Ephedraceae	Ephedrine	Alkaloid	Bronchodilator, stimulant
Pilocarpus species	Jaborandi	Rutaceae	Pilocarpine	Alkaloid	Glaucoma
Podophyllum peltatum	May-apple	Berberidaceae	Podophyllotoxin, etoposide	Resin	Anticancer
Rauwolfia serpentina		Apocynaceae	Reserpine	Alkaloid	Antihypertensive, tranquilizer
Taxus brevifolia	Pacific yew	Taxaceae	Taxol	Diterpene	Anticancer (ovarian, breast)

How Plant Pharmaceuticals Are Discovered

ethnobotany the study of traditional uses of plants within a culture

biodirected assays tests that examine some biological property

The search for new pharmaceuticals from plants is possible using a number of distinct strategies. Random collecting of plants by field gathering is the simplest but least efficient way. The chances are much greater that new compounds of medicinal value will be discovered if there is some degree of selectivity employed by collecting those plants that a botanist knows are related to others already having useful or abundant classes of secondary metabolites. Even more relevant is to collect plants already targeted for specific medicinal purposes, possibly among indigenous or ethnic peoples who use traditional, plant-derived medicines often with great success to provide for their well-being. Such data are part of **ethnobotany**, when researchers often obtain detailed information on the plants people use to treat illnesses, such as the species, specific disease being treated, plant part preferred, and how that part is prepared and used for treatment. This strategy can provide rapid access to plants already identified by traditional practitioners as having value for curing diseases, and this shortcut often sets the researcher rapidly on the road to the discovery of new drugs.

Taking the ethnobotanical approach, a specific part of the targeted ethnomedicinal plant is extracted, usually in a solvent like ethanol, and then studied in **biodirected assays** or tests to determine its value using, for instance, tissue cultured cells impregnated with the organism known to cause the disease. For example, to assay for malaria the procedure could involve culturing red blood cells infected with the malarial-causing protozoan *Plasmodium falciparum*, placing a few drops of extract into the culture, and examining after a few days what effect, if any, the addition of the extract had on the protozoa. One final step in this process leading to the discovery of a new drug is to establish the mechanism of action of the compound, reactions in the body, and side effects or toxicity of taking it. The whole process from field discovery to a new pharmaceutical takes up to ten years and requires a multidisciplinary-interactive approach involving **ethnobotanists**, natural products chemists, pharmacognosists (those who study the biochemistry of natural products), and cell and molecular biologists.

A May-apple (*Podophyllum peltatum*).

ethnobotanist a scientist who interacts with native peoples to learn more about the plants of a region

Medically Important Compounds Derived From Plants

About ninety species of plants contribute the most important drugs currently used globally, and of these about 75 percent have the same or related uses as the plant from which each was discovered. Two examples provide additional details of their discovery and development as drugs.

May-apple. Eastern North American Indians long used the roots and rhizomes (underground stems) of the native May-apple (*Podophyllum peltatum*, Berberidaceae) as a drastic laxative. By the nineteenth century, white "Indian Doctors" used extracts of these parts to treat cancerous tumors and skin ulcers, perhaps learned from Indians or by direct observation of its corrosive and irritating nature. The plant's main secondary metabolite is podophyllotoxin, a resin responsible for May-apple's antitumor effects. It is a mitotic poison that inhibits cell division and thus prevents unregulated growth leading to cancerous cells and tumors. However, in clinical trials podophyllotoxin proved too toxic for use as a cancer chemotherapeutic agent, although it remains the drug of choice as a caustic in removing venereal warts and other benign tumors.

Attempts to find safer compounds led chemists to manipulate the molecule, and by trial and error they discovered a semisynthetic derivative that proved at least as effective as the original compound without the same level of toxicity. (Semisynthetics are products of chemical manipulation using the naturally occurring plant compound as a base.) A compound called etoposide was eventually found most valuable in treating a type (non-small cell) of lung cancer, testicular cancer, and lymphomas (cancer of lymphoid tissue), and particular (monocytic) leukemias (cancer of blood-forming organs) by preventing target cells from entering cell division. Etoposide was approved for use in the United States in 1983, twelve years after its discovery. Peak annual sales of the compound reached approximately $300 million in the late 1980s and early 1990s, and thousands of lives have been prolonged or saved during nearly two decades of its use as a leading anticancer drug derived from plants. It is possibly the most important pharmaceutical originating from a plant species native to eastern North America.

Foxgloves. Heart and **vascular** disease is the number one killer in the United States, a position held virtually every year in the twentieth century. Fluid accumulation or edema (dropsy) and subsequent congestive heart failure have been treated by European farmers and housewives as part of European folk medicine for a long time. Their remedy consisted of a concoction of numerous herbs that always contained leaves of foxglove (*Digitalis* species, Scrophulariaceae). In the 1700s William Withering, an English botanist and physician, observed in the countryside the successful use of this herbal mixture to treat dropsy and associated diseases. He eventually se-

vascular related to blood vessels

A foxglove (*Digitalis purpurea*).

cardiotonic changing the contraction properties of the heart

systematists scientists who study systematics, the classification of species to reflect evolutionary relationships

lected one plant from the mixture as the probable source of activity, and in 1785 Withering published his landmark book *An Account of the Foxglove, and Some of Its Medicinal Uses* in which he described how to determine the correct dosage (for foxglove was considered a potent poison that was ineffective medicinally unless used at near toxic levels) and how to prepare foxglove, favoring the use of powdered leaves.

Withering's discovery revolutionized therapy associated with heart and vascular disease, and even today, powdered foxglove leaves are still prescribed and used much as they were more than two centuries ago. The active leaf metabolites are **cardiotonic** glycosides obtained mostly from two European species, *Digitalis lanata* and *D. purpurea*. They provide the most widely used compounds, digoxin (also available synthetically), digitoxin, and lanatosides. The magnitude of the need for cardiotonic therapy is suggested by the estimate that more than three million cardiac sufferers in the United States routinely use the preferred digoxin as one of several available drugs.

In congestive heart failure, the heart does not function adequately as a blood pump, giving rise to either congestion of blood in the lungs or backup pressure of blood in the veins leading to the heart. When the veins become engorged, fluid accumulates in the tissues, and the swelling is known as edema or dropsy. Cardiotonic glycosides increase the force of heart muscle contraction without a concomitant increase in oxygen consumption. The heart muscle thus becomes a more efficient pump and is better able to meet the demands of the circulatory system. If heart failure is brought on by high blood pressure or hardening (loss of elasticity) of the arteries, cardiotonic glycosides are also widely used to increase contractibility and improve the tone of the heart muscle, resulting in a slower but much stronger heart beat. If the heart begins to beat irregularity, again these cardioactive compounds will convert irregularities and rapid rates to normal rhythm and rate.

The search for new medicinal plants continues as remote regions of natural habitat are explored by botanists, plant **systematists**, and ethnobotanists. Further clinical studies of chemical components of these new discoveries may yield important novel drugs for the treatment of human diseases. SEE ALSO ALKALOIDS; CANNABIS; COCA; DIOSCOREA; ECONOMIC IMPORTANCE OF PLANTS; ETHNOBOTANY; HERBALS AND HERBALISTS; OPIUM POPPY; PHARMACEUTICAL SCIENTIST; PLANT PROSPECTING; PSYCHOACTIVE PLANTS; SYSTEMATICS, PLANT.

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Mendel, Gregor

Austrian Natural Scientist
1822–1884

Gregor Mendel.

Gregor Mendel elucidated the theory of particulate inheritance, which forms the basis of the current understanding of genes as the hereditary material. Born in Heinzendorf, Austria, in 1822, Johann Gregor Mendel was the fourth of five children in a family of farmers. He attended the primary school in a neighboring village, which taught elementary subjects as well as the natural sciences. Mendel showed superior abilities, and in 1833, at the advice of his teacher, his parents sent him to the secondary school in Leipnik, then to the gymnasium in Troppau. There he attempted to support himself by private tutoring, but his lack of the necessary financial support made the years that Mendel spent in school extremely stressful for him. His younger sister gave him part of her dowry and, in 1840, he enrolled in the University of Olmütz, where he studied physics, philosophy, and mathematics. In 1843 he was admitted into the Augustinian monastery in Brno, where he stayed for almost two decades. Originally, Mendel was not interested in religious life, but joining the monastery freed him from the financial concerns that plagued him and allowed him to pursue his interests in the natural sciences.

Under the leadership of its abbot, F. C. Napp (1792–1867), the monastery in Brno integrated higher learning and agriculture by arranging for monks to teach natural sciences at the Philosophical Institute. Napp encouraged Matthew Klácel to conduct investigations of variation and heredity on the garden's plants. Klácel, a philosopher by training, integrated natural history and Hegelian philosophy to formulate a theory of gradual development. This work eventually led to his dismissal, and he immigrated to the United States. Mendel was put in charge of the garden after Klácel's departure.

From 1844 through 1848 Mendel took theological training as well as agricultural courses at the Philosophical Institute, where he learned about artificial pollination as a method for plant improvement. After he finished his theological studies, Mendel served a brief and unsuccessful stint as parish chaplain before he was sent to a grammar school in southern Moravia as a substitute teacher. His success as a teacher qualified him for the university examination for teachers of natural sciences, which he failed because of his lack of formal education in zoology and geology. To prepare himself to retake the test, he went to the University of Vienna, where he enrolled in courses in various natural sciences and was introduced to botanical experimentation. After completing his university training he returned to Brno and was appointed substitute teacher of physics and natural history at the Brno technical school.

Mendel was an excellent teacher, and he often taught large classes. In 1856 he began botanical experiments with peas (*Pisum*), using artificial pollination to create **hybrids**. Hoping to continue his education, he once again took the university examination, but failed and suffered an emotional and physical breakdown. His second failure spelled the end of his career as a student, but he remained a substitute teacher until 1868, when he was elected abbot of the monastery. Mendel stayed in Brno, serving the monastery, performing botanical experiments, and collecting meteorological information until he died of kidney failure in 1884. At the time of his death, he was well

hybrid a mix of two varieties or species known for his liberal views and his conflict with secular authorities over the setting aside of monastery land; at this time, only the local fruit growers knew him for his botanical research.

Experiments on Inheritance

While his contemporaries knew little of his scientific work, Mendel's historical significance lies almost entirely in his experimental work with the **hybridization** of plants and his theory of inheritance. Beginning in 1856 and continuing through 1863, Mendel cultivated nearly thirty thousand plants and recorded their physical characteristics. Beginning with a hypothesis about the relationship between characteristics in parents and offspring, Mendel formulated an experimental program.

hybridization formation of a new individual from parents of different species or varieties

Mendel believed that heredity was particulate, that attributes were passed from parents to offspring as complete characters. His notions of heredity were contrary to the belief in blending inheritance, which was generally accepted at the time and explained the attributes of an organism as a blended combination of its parents' characters. Instead of viewing an organism's individual characteristics as composites of its predecessors, Mendel asserted that organisms inherited entire characters from either one or the other parent. To test his theory, he chose seven plant and seed characteristics, such as the shape of the seed or the color of the flower, and traced the inheritance of the characters through several generations of pea plants.

As he crossed thousands of pea plants and recorded the seven characteristics, Mendel found that certain traits were passed from parent to offspring in a lawlike fashion. Just as he had hypothesized, certain traits regularly appeared when he crossed plants with different combinations of characteristics. He used the term "dominant" in reference to those traits that were passed from the parent to the offspring and the term "recessive" in reference to those traits that were exhibited in at least one of the parents, but not in its offspring. Mendel denoted plants with dominant traits by recording two capital letters, such as AA, and those that expressed recessive traits with lower case letters, like aa. In the first generation of offspring from crosses of AA with aa, dominant traits always appeared and recessive traits never appeared.

Mendel's system of denoting dominant and recessive traits with two letters allowed him to trace dominant and recessive characters through successive generations. The crossing of AA with aa would result in the production of individuals with traits represented by Aa, with the dominant trait always appearing, but not the recessive trait. By crossing two Aa individuals, Mendel found that the dominant trait appeared three times for every one time that the recessive trait appeared. Mendel explained that the crossing of two Aa individuals resulted in the production of the following combinations:

AA Aa Aa aa

Because the dominant trait always decided the characteristic, any organism with at least one A would express the dominant trait. Recessive characteristics would appear only in those individuals with aa.

Mendel's 1866 "Versuche über Pflanzenhybriden" (Attempts at Plant Hybridization) presented his entire theory of inheritance and has become one of the most significant papers in the history of biology. He explained that his results "were not easily compatible with contemporary scientific knowledge" and, as such, "publication of one such isolated experiment was doubly dangerous, dangerous for the experimenter and for the cause he represented." In an attempt to bolster his case, Mendel experimented on several other plants and then with animals. However, after 1866 he published only one more short article on the subject.

Rediscovery of Mendel's Work

Mendel's painstaking experimental work on plant hybridization and heredity sat virtually unnoticed for thirty-five years before three natural scientists simultaneously rediscovered it at the turn of the twentieth century. His 1865 paper, presented at the Natural Sciences Society of Brno and published in the Society's *Verhandlungen* in 1866, received little notice from his contemporaries. However, in 1900 Carl Correns, Erich von Tschermak, and Hugo DeVries, each working independently, found Mendel's paper while they were each in the process of completing similar experiments. In the hands of a new generation of natural scientists, Mendel's work was immediately and widely accepted, and he was touted as the epitome of a scientist.

Mendelism, as his work was called, was often posited in opposition with the Darwinian theory of natural selection. Many early twentieth-century Mendelians and Darwinians believed that the two theories were incompatible with one another, in part because of Darwin's reliance on the theory of **pangenesis** and because contemporary biologists, who also viewed Darwinism in conflict with DeVries's mutationism, associated Mendel's work with mutationism.

pangenesis the belief that acquired traits can be inherited by bodily influences on the cells

Despite the debates over the relationship between Mendelism and Darwinism, Mendel's work immediately received widespread support, and it served as the basis for work in genetics as well as plant and animal breeding. Beginning around 1900, Mendelism also provided a substantial boost to the growing science of eugenics, the genetic improvement of humans by encouraging "high-quality" individuals to have children while discouraging "low-quality" people from reproducing. By scientifically explaining inheritance, Mendelism bolstered the eugenicists' claim that "good begets good and bad begets bad." Later geneticists distanced themselves from eugenics by arguing that, while Mendelism easily explained simple traits like eye color or blood type, it did not apply to more complicated traits like intelligence or industriousness.

Beginning in the late 1930s, yet another generation of natural scientists reinterpreted Mendelism and Darwinism, and they concluded that they were mutually reinforcing scientific theories. R. A. Fisher, Sewall Wright, J. B. S. Haldane, and other so-called synthesis biologists argued that Mendelism provided the explanation for one facet of evolution, inheritance, while Darwinism explained another, selection. Viewed in this light, Mendel's work complemented Darwin's theory of natural selection, and the two have served as the principal basis for modern biological thought since the mid-twentieth century. SEE ALSO CHROMOSOMES; DARWIN, CHARLES; GENETIC MECHANISMS AND DEVELOPMENT.

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Meristems

apical at the tip

lateral away from the center

Meristems are regions of active cell division within a plant. In general there are two types of meristems: **apical** meristems and **lateral** meristems. Apical meristems are located at the tip (or apex) of the shoot and the root, as well as at the tips of their branches. These meristems occur in all plants and are responsible for growth in length. By contrast, lateral meristems are found mainly in plants that increase significantly in diameter, such as trees and woody shrubs. Lateral meristems are located along the sides of the stem, root, and their branches; are found just inside the outer layer; and are responsible for growth in diameter.

The term *meristem* comes from the Greek word meaning "divisible," which emphasizes the fundamental role played by mitotic cell division in these tissues. Meristematic cells are those that divide repeatedly and in a self-perpetuating manner; that is, when a meristematic cell divides, one of the daughter cells remains meristematic. Meristems, however, may not be constantly active. For example, in temperate climates meristematic cells stop dividing during the winter but then begin dividing again in the spring.

Apical Meristems

Both root and shoot apical meristems consist of a group of two types of cells: initials and their immediate derivatives. Initials are the true meristematic cells in that they divide almost continuously throughout the growing season. When an initial divides it forms two daughter cells, one a new initial and the other a derivative that soon stops dividing and eventually differentiates into part of the mature tissues of the plant. In many cases the older derivatives elongate, and it is this process that pushes the initials of the shoot apical meristem higher into the air and the initials of the root apical meristem deeper into the soil. All tissues produced by an apical meristem are called primary tissues.

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Use for storage and maintaining internal pressure

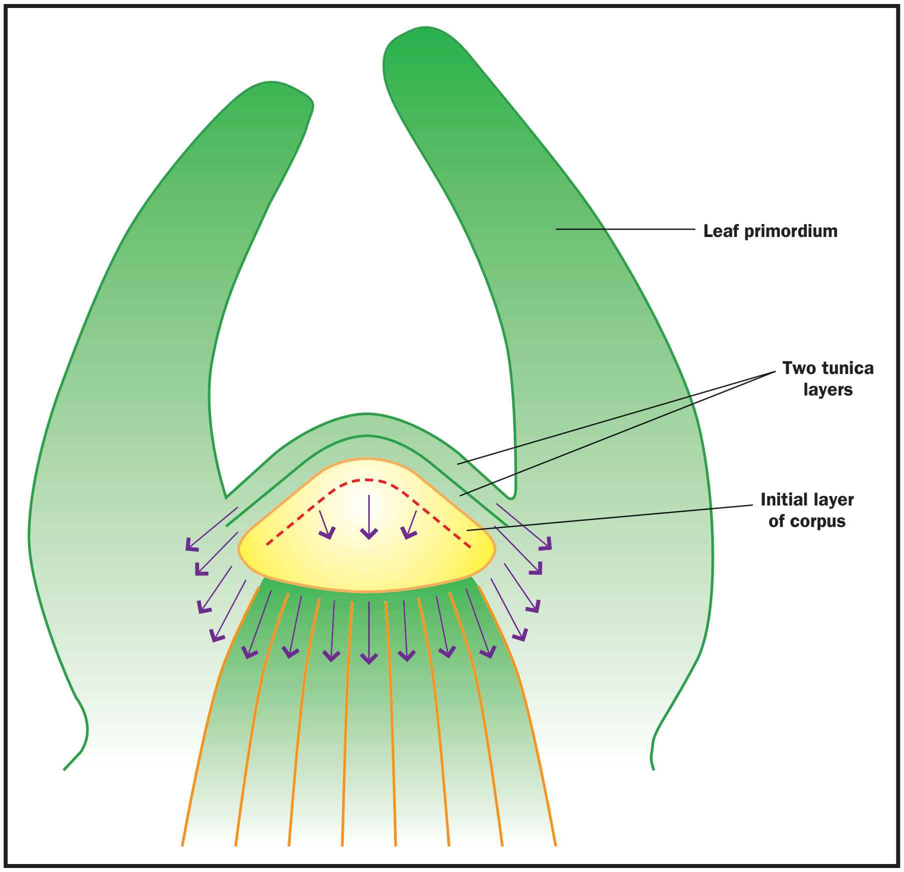
epidermis outer layer of cells

In most plants the root apical meristem is covered by a protective root cap and consists of a group of relatively small, roughly spherical cells, each having a dense cytoplasm and a large nucleus but no apparent **vacuole**. The derivatives of certain apical initials give rise to additional root cap cells, thus replacing those that were lost as the root cap rubbed against soil particles. The derivatives of other initials give rise to the mature tissues of the main body of the root, such as xylem, phloem, cortex, and **epidermis**. In the center of the root apex is a cluster of cells that divides very infrequently. These cells comprise the quiescent center, whose apparent function is to serve as a source of cells should the initials become damaged.

angiosperm a flowering plant

primordia the earliest and most primitive form of the developing leaf

In **angiosperms**, the shoot apical meristem is not covered by a protective cap and has additional features that distinguish it from the root apex. For example, the lateral appendages of the stem—the leaves and lateral buds—are produced at the shoot apex. Leaves arise as small protuberances (called leaf **primordia**) slightly to the side of the apical-most cells. As they



A schematic diagram of the apical meristem, showing the directions of cell division.

elongate, the resulting leaves cover and protect the apical meristem. Buds develop in the angle between the stem and each leaf primordium, a location called the leaf axil. In a plant growing vegetatively, these **axillary** (or lateral) **buds** contain meristems that can develop into branches. When the plant reproduces sexually, the shoot apical meristem produces flowers instead of leaves. The various flower parts—petals, **sepals**, stamens, and **carpels**—are modified leaves and are produced in a manner similar to that of leaf primordia.

axillary bud the bud that forms in the angle between the stem and leaf

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

The apical meristem of most angiosperms has a tunica-corpus arrangement of cells. The tunica consists of two or more layers of cells, and the corpus is a mass of cells underneath. Cells of the tunica and corpus give rise to the leaves, buds, and mature tissues of the stem.

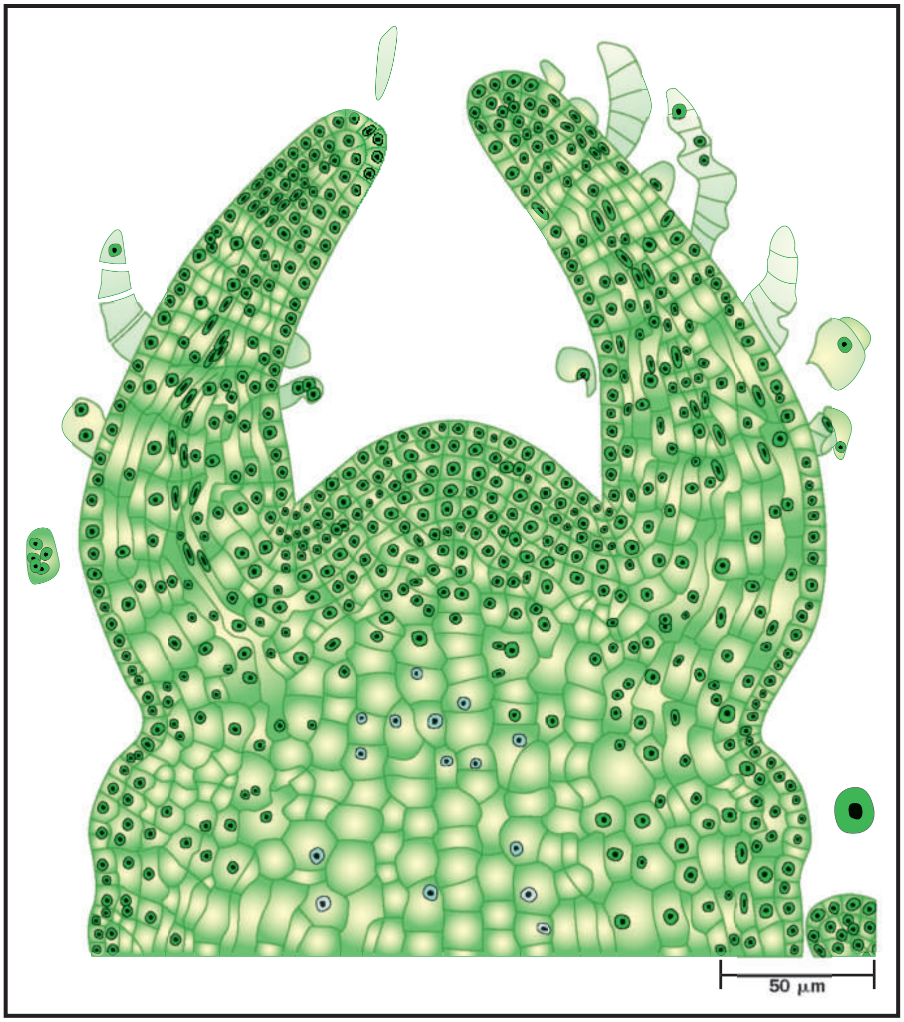
Lateral Meristems

Two types of lateral meristems, also called cambia (singular: cambium), are found in plants: the **vascular** cambium and the cork cambium. Each type consists of a hollow, vertical cylinder of cells that contribute to the thickness of woody plants. As with apical meristems, lateral meristems consist of initials and their immediate derivatives. All tissues produced by a lateral meristem are called secondary tissues.

vascular related to transport of nutrients

The vascular cambium contains two kinds of initials: fusiform initials and ray initials, both of which have large vacuoles. Each type of initial produces derivatives toward the inside that develop into xylem cells and deriv-

Tunica-corpus arrangement of cells. Redrawn from Raven et al., 1999, Figure 26–4.

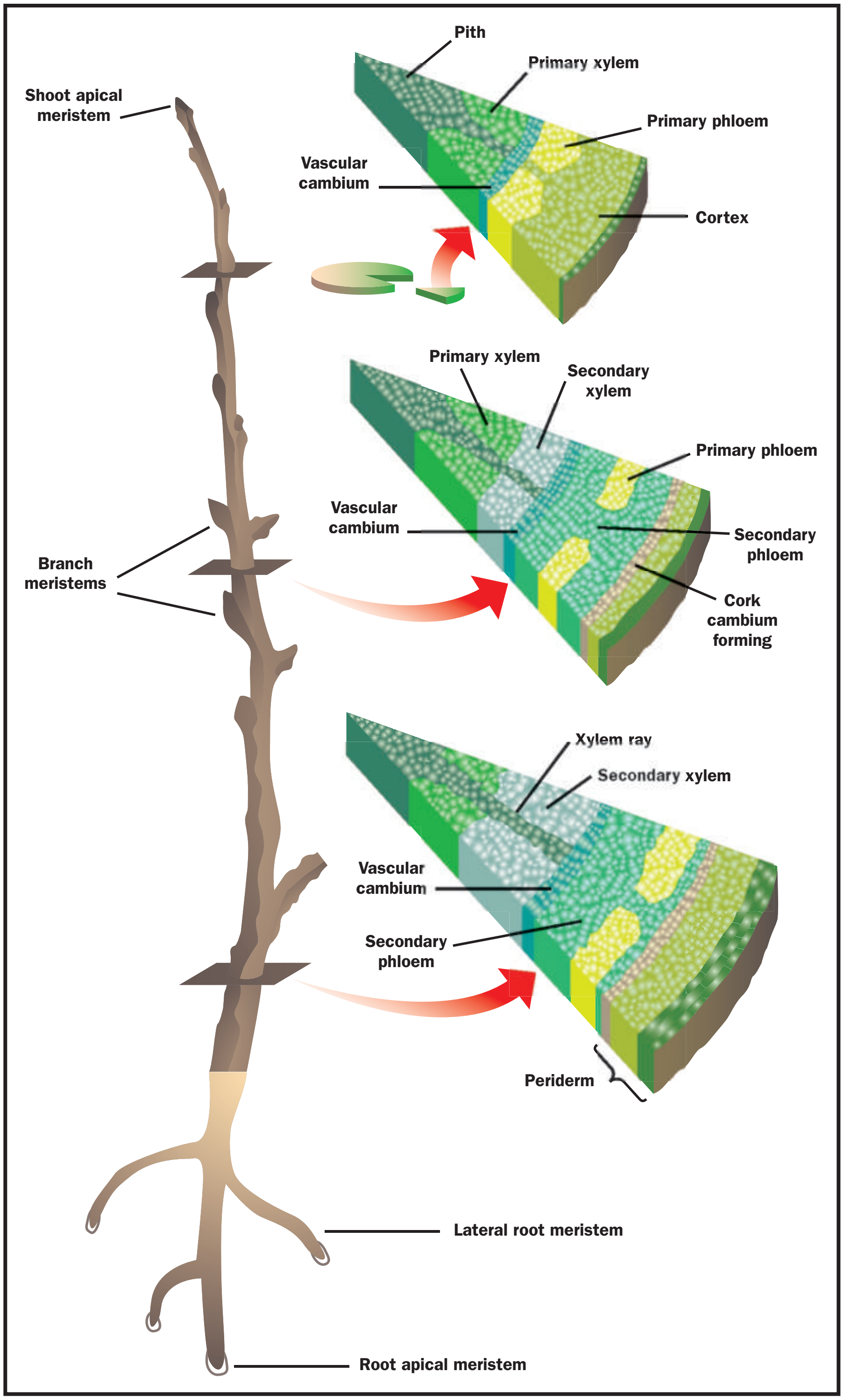


atives toward the outside that develop into phloem cells. The fusiform initials are long, tapering cells that are vertically oriented. They give rise to xylem vessel elements and phloem sieve-tube members; these cells are involved in the vertical transport of materials through the plant. The ray initials are cube-shaped cells that give rise to xylem **parenchyma** and phloem parenchyma and together constitute the vascular rays. Rays are involved in the lateral transport of materials. Both the fusiform and ray initials produce many more xylem cells than phloem cells. The accumulating xylem cells push the vascular cambium increasingly farther away from the center of the root, stem, or branch, and as a result the organ increases in diameter.

parenchyma one of three plant cell types

In response to this increase in thickness the epidermis and other cells exterior to the vascular cambium stretch and eventually break. Before cracks occur, a cork cambium differentiates from cells of the cortex. The cork cambium (or phellogen) produces cork cells (phellem) toward the outside and phelloderm toward the inside. Together, these three tissues constitute the periderm. Cork cells have a flattened shape, and their walls become filled with suberin, a fatty material that makes these cells an impermeable barrier to water, gases, and **pathogens**. Although the cork cambium and phelloderm are alive at maturity, cork cells are dead. The cork thus provides an effective seal that replaces the epidermis. As the plant organ con-

pathogen disease-causing organism



Meristem locations, with cross-sections of vascular tissues. Redrawn from Moore et al., 1998, Figure 16.1.

tinues to increase in diameter, the cork cells themselves crack, and additional cork cambia differentiate from underlying tissues as replacements. SEE ALSO Anatomy of Plants; Bark; Cells, Specialized Types; Differentiation and Development; Germination and Growth; Tissues; Vascular Tissues.

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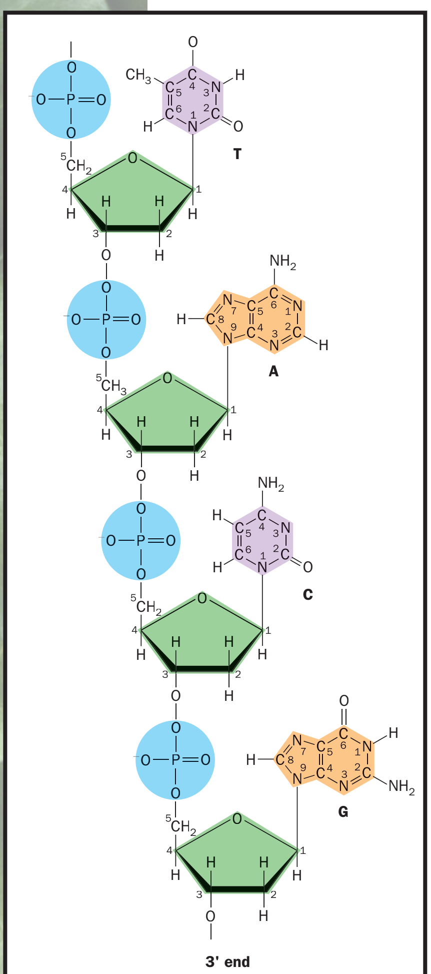
Mold *See Fungi*

Molecular Plant Genetics

The appearance and chemical composition of all life are determined by the action of genes functioning in the context of the conditions surrounding the organism. While both genes and environment are important in determining the characteristics of plants, it is becoming clearer that genes control many more characteristics, and to a higher degree, than we had previously imagined. Hence, the study of genes and their effects on organisms, genetics, has allowed us to combat a wide range of human diseases. The burgeoning plant biotechnology industry, which promises to produce revolutionary plants and plant products in the twenty-first century, has also arisen. An intriguing tenet of modern genetics is that the cellular molecules that carry the genetic information (deoxyribonucleic acid [DNA]) and transmit this data to cells (ribonucleic acid [RNA] and proteins) are the same in plants and animals, so that geneticists speak one universal language that can be interpreted and manipulated, through science, to beneficially alter any species.



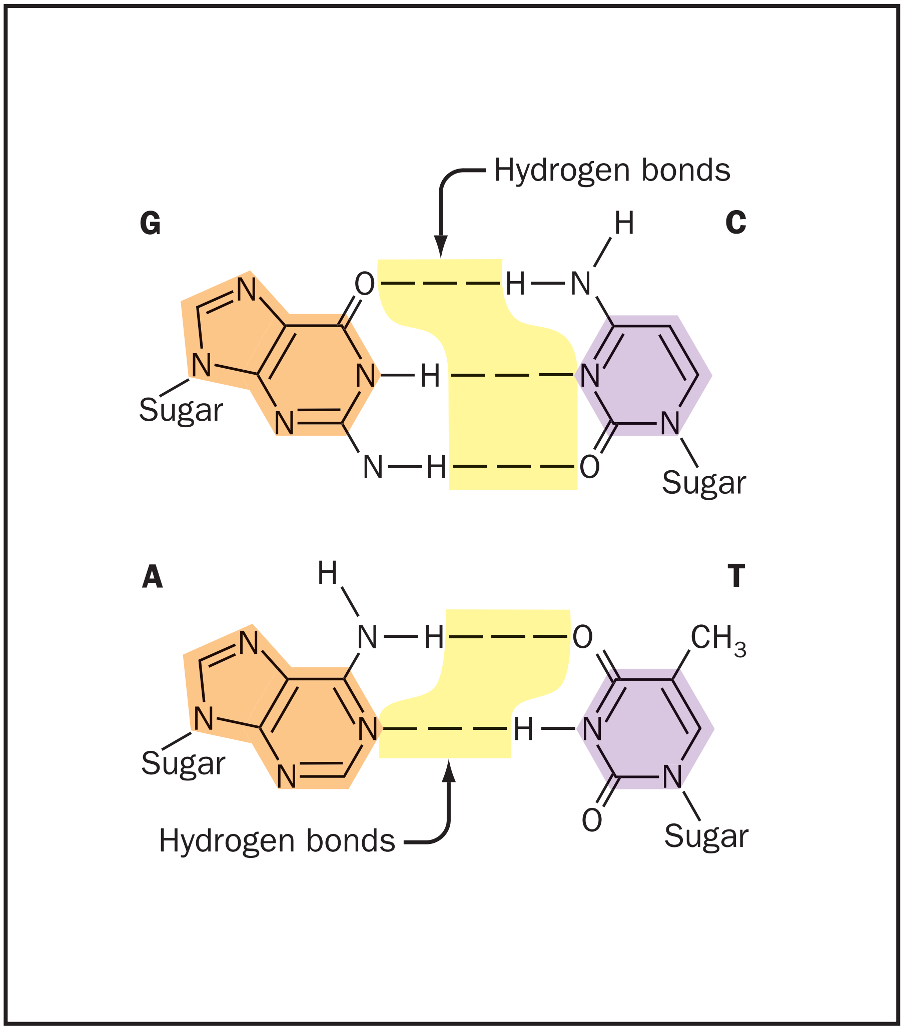
DNA sugar-phosphate backbone with linked bases.

DNA, Genes, and Chromosomes

DNA is the molecule that constitutes genes. The main component of each cell's DNA is found in its nucleus. The individual, very large DNA molecules of the nucleus are chromosomes, each of which consists of thousands of genes, and each cell of an individual plant species has the same DNA and chromosomal composition. Copies of all genes are transmitted from both parents to their offspring, accounting for inheritance, the principle wherein offspring resemble their parents.

The chemical structure of DNA allows it to store information and for that information to be incorporated into the design of developing cells and organs. DNA molecules are very long linear structures comprised of millions of repeating units. Segments, consisting typically of a few thousand of these units, constitute individual genes. Each gene carries the information that dictates the structure of a single protein. Proteins catalyze all of the chemical reactions in cells generating its components and forming the cells into recognizable tissues and organs.

The backbone of a DNA molecule consists of alternations of the 5-carbon sugar, 2-deoxyribose, and phosphate. Note that the sugars are linked at their number three position (3′, read as "three prime") to a phosphate and their number five position (5′) at the other end to another phosphate. Further, the sugars are all oriented by these links in the same di-



Paired bases of DNA showing the weak bond (dotted lines) that holds them together.

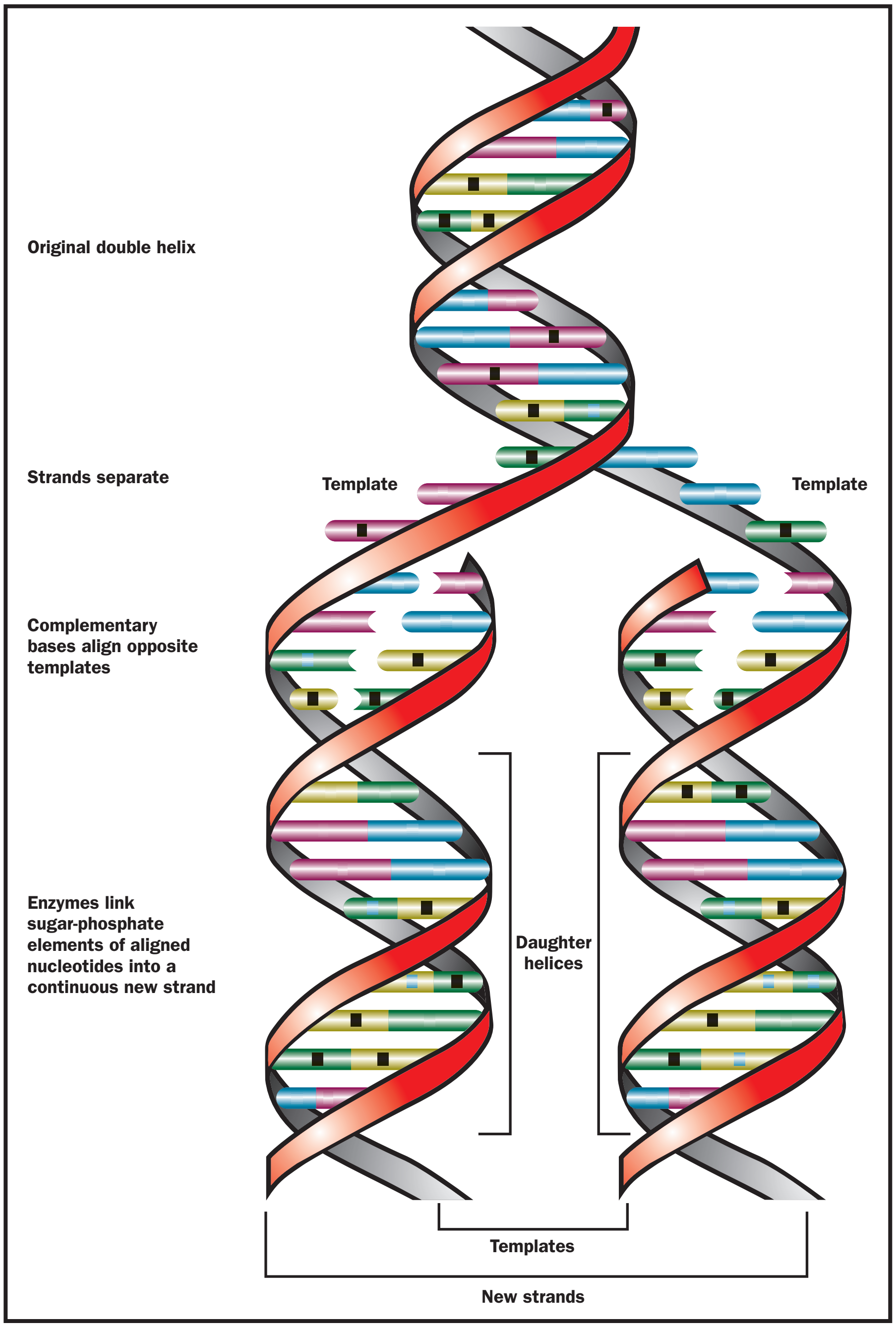
rection so that the backbone has direction—that is, a 5′ and a 3′ end. Connected to each sugar, at its 1′ position, is one of four nitrogenous bases: adenine, cytosine, guanine, or thymine. Each DNA backbone is actually paired for its full length with a second DNA backbone, with the chemical linkage between the two occurring via weak hydrogen bonding between the bases of the two chains. Two aspects of this pairing should be noted: 1) the two sugar-phosphate backbones have opposite orientations (they are antiparallel); and 2) any adenine of either chain is bonded (paired) with a thymine, and each guanine is paired with a cytosine. Consequently, the sequence of bases of the two chains are complementary to one another so that one can be predicted from the other. It is the sequence of bases within a gene that determines the type of protein that the gene codes for, including the protein's function in plant cells. Within a gene for a particular protein, three successive bases determine one amino acid. For example, A (abbreviation for adenine), followed by T (thymine), and then G (guanine) code for the amino acid methione (ATG is the term for this code in DNA sequence terminology), and each of the twenty possible amino acids that are incorporated into proteins have their own three-base determinants, or codons. For most amino acids, there are several three-base sequences that will code for a particular amino acid.

Replication

For DNA to function as a hereditary molecule, it must be duplicated (replicated) so that the daughter cells produced by cell division can receive identical copies. Replication of DNA is accomplished by a large complex of **enzymes**, within which the main replication enzyme, DNA polymerase, carries out the main synthesizing reaction. In DNA replication, the following steps are accomplished by the synthesis complex:

enzyme a protein that controls a reaction in a cell

1. the two halves of the starting double-stranded DNA, which are wound together in a ropelike helix, are separated so that the bases are exposed;



A DNA molecule being replicated.

2. the replication complex reads each half of the unwound DNA so that molecules complementary to each of original halves of the helix are synthesized from new subunits; and
3. these new chains are left bonded to old ones so that there are now two half-new, half-old identical DNAs. DNA replication must occur in each cell before the cell can divide and is also necessary in reproduction prior to the generation of pollen grains and ovules.

Protein Synthesis

The process by which genes are read and the sequence used to form a **polymer** of amino acids in a protein consists of two steps. In the first transcription, a copy of the gene is made in the form of RNA. Then, via the process of translation, the RNA sequence is interpreted by the translation machinery to make the actual protein. RNA is a molecule that is similar to DNA in structure, with the following differences: 1) its sugar is ribose, also a 5-carbon molecule, but which has an OH group at the 2′ position, 2) it is usually single stranded, rather than consisting of two paired strands, and 3) it utilizes the base uracil in place of thymine, which does have similar base pairing characteristics. Hence, RNA has a similar, but not identical, sugar-phosphate backbone to DNA, and the sequences of bases in its structure can convey information in the same fashion.

polymer a large molecule made from many similar parts

In a biochemical sense, the events of transcription (DNA-dependent RNA synthesis) are similar to the steps of DNA replication. The paired halves of the DNA constituting one end of the gene are separated, and an enzyme complex is attached. Included in this complex is an enzyme called RNA polymerase that reads the DNA and builds an RNA molecule having a base sequence complementary to that of the template DNA.

Once the RNA copy, called messenger RNA (mRNA), is made in a plant nucleus, it undergoes several modifications and is then transmitted to the cytoplasm. Here, the mRNA is utilized by the process of translation that generates a protein having an amino sequence corresponding to the base sequence of the mRNA and its gene. The process of translation, or protein synthesis, takes place on ribosomes, which are composed of ribosomal RNA (rRNA) and more than one hundred proteins. The ribosome attaches to an mRNA and moves along its length, synthesizing a protein by adding the correct amino acids, in sequence, one at a time. The addition of the correct amino acid at each point is accomplished by the pairing of three bases of the mRNA with a transfer RNA, which has a three-base segment complementary to this set of bases and which was previously attached to the correct amino acid by an enzymatic reaction. Consequently, the correct functioning of transcription and translation allows the information of each gene to be interpreted and converted into a protein, which carries out a very specific metabolic reaction in the cell.

Polyploidy

An interesting feature of plant chromosomes that is much less common in animals is polyploidy. Polyploidy occurs when the entire set of chromosomes is multiplied, relative to the normal two of each kind per cell. For example, the normal **diploid** number of corn chromosomes is

diploid having two sets of chromosomes, versus having one (haploid)

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower twenty; that is, each cell of a normal plant contains two of each of ten different chromosomes. If this number were doubled so that there were a total of forty, with each of the ten different types being represented four times, the result would be tetraploid corn containing four of each chromosome. The common peanut is a natural tetraploid species. Polyploid strawberries have been created artificially to increase the desirable characteristics of the fruit.

Mutations and Polymorphisms

Any change in a DNA molecule of a plant or animal is called a mutation, whether occurring in nature or induced experimentally. Changes in DNA occur in nature as a result of either environmental agents or rare but inevitable mistakes in the DNA replication process. The resulting natural variations of DNA sequence among the individuals of a species, DNA polymorphisms, fuel evolution. These polymorphisms can be analyzed through molecular techniques and can be used to determine the relationship among plants and molecular plant improvement as well as identifying individual plants. Hence, we have seen the development of DNA fingerprinting for intellectual property protection of novel genetic improvements in plant breeding—which is similar to the fingerprinting techniques used in several human criminological contexts.

Specific mutational changes in DNA may affect the function of the resulting protein, usually by reducing its efficiency or rendering it completely nonfunctional. However, in rare cases, a mutation may make the enzyme more useful for metabolism in some way. The former type of change is widely used by plant scientists to discover the roles of genes in growth and development; the latter represents the goal of protein engineering and is the basis of plant biotechnology.

Uses of Mutants

The genetic dissection of plant growth and development is one of the outstanding uses of mutations for scientific analysis. For example, a number of mutants block aspects of flower development. One mutant was discovered whose flowers lack petals, another lacks both the male and female reproductive parts of the flower, and still another lacks **sepals** and petals. Detailed analysis of the effects of these mutants, along with the cloning and characterization of the genes themselves, has led to a partial understanding of how a plant makes flowers. It is likely that a complete picture will eventually result. Interestingly, the original flower development model was developed for the small dicot, *Arabidopsis*, which has both sexes in one flower, but the same regulators act in the crop plant corn, which has separate male and female flowers, and which are completely different in appearance from those of *Arabidopsis*.

Another experimental application of mutant analysis illustrates the use of genetics in biotechnology and the generation of transgenic plants. Plants are said to be transgenic when DNA from some external source is introduced by scientists through biotechnology. In this case, a mutation was discovered in *Arabidopsis* called "leafy." This mutation is a loss-of-function change, which results in the replacement of flowers and fruits by leaves. Hence, the normal version of this gene must promote the ability to produce

ARABIDOPSIS

Arabidopsis thaliana is a small plant that has played a large part in unraveling the molecular genetics of plants. It has an approximately two- to four-inch-wide cluster of leaves and a several-inch-tall flowering structure and is capable of producing thousands of tiny seeds within four to six weeks after germination. Because of its small size and short generation time, it has long been used for genetic research. In the 1980s it was discovered that the deoxyribonucleic acid (DNA) content of its genome was very small, and it was therefore adopted as the favorite model for basic study of molecular control of plant development and metabolism. In the 1990s more research was published on *Arabidopsis* than on any other plant. Further, as biotechnology has developed, it was realized that a model organism could form the focus for initial evaluation of key systems, and several startup biotechnology firms that have substantial *Arabidopsis* research components have been established.

A new biological discipline called genomics has recently arisen. A genome is defined simply as the entire set of chromosomes (and thus DNA) of a species. Genomics is the analysis of the entire set (or at least a very large subset) of an organism's genes. Plant genomics is made possible by two circumstances: 1) the capability to clone and determine the base sequence of the entire length of all of the chromosomes of a plant, and 2) the development

(continued on page 85)

flowers. Subsequently, the normal gene was cloned and inserted into different plant species by transgenic techniques. When poplar trees received the gene, the genetically modified tree seedlings germinated normally but flowered within months rather than several years later, as occurs in normal trees.

Transgenically modified plants used in agriculture are often referred to as GMOs or genetically modified organisms. An example of GMOs are Roundup-Ready soybeans, which have resistance to this effective, nonpolluting herbicide through a transgene. These beans are widely used but are somewhat controversial. The public debate over the use of GMOs in agriculture involves a number of complex political issues in addition to the public health and environmental concerns that may also be relevant for certain types of GMOs. The handling of this issue represents one of the important public policy issues of our era. Another example of a potentially beneficial GMO is rice that is altered to carry more iron in its seeds. This should dramatically improve its nutritional value and prove especially valuable in areas of the world where food is scarce and human diets are typically not well balanced.

Improvement of crop plants has been practiced by plant breeders for centuries. The molecular tools discussed above simply enhance the range of alterations that are possible for improving crops. Traditional crop breeding involves finding and evaluating potentially useful genetic variants of a species, intercrossing them so that the most optimal set of characteristics can be combined into one strain, and then evaluating a number of resulting strains for final use in actual production farming. This is a long and costly process. In addition, many of the traits, which are of interest from an agronomic perspective, are quantitative as opposed to qualitative in inheritance. That is, they are controlled by large numbers of genes, each of which has a relatively small effect on performance. When this is the case, the application of classical genetics and molecular biology is difficult, since individual genes affecting a quantitative trait are very difficult to identify or clone. However, molecular markers can be correlated with important quantitative traits of a segregating population and utilized to pinpoint the general chromosomal locations where greater-than-average effects on the quantitative traits are exerted. Loci found in this way are referred to as quantitative trait loci or QTLs. QTL approaches are being pursued in many crops as alternative means of developing improved crop varieties and understanding the genetic basis of quantitatively inherited traits. SEE ALSO BREEDING; CELL CYCLE; CHROMOSOMES; CREIGHTON, HARRIET; GENETIC ENGINEER; GENETIC ENGINEERING; GENETIC MECHANISMS AND DEVELOPMENT; MCCLINTOCK, BARBARA; MENDEL, GREGOR; POLYPLOIDY; QUANTITATIVE TRAIT LOCI; TRANSGENIC PLANTS; WARMING, JOHANNES.

Randy Scholl

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of new technologies to assay whether genes are being transcribed on a genome-wide scale. The *Arabidopsis* Genome Initiative (AGI), an international collaboration, was established in 1995 with the goal of determining the DNA base sequence of the entire *Arabidopsis* chromosome set (genome). By the time the project finished in 2000, all of the estimated twenty thousand plus genes of this plant were available for molecular and biological analyses.

Given the availability of the complete genomic sequence data, the next focus of international *Arabidopsis* cooperation is functional genomics. Functional genomics is simply the analysis of genes and their effects on the full scale of the entire genome, that is, all (or most) of the genes at once. In one of the most powerful full-genome approaches, microarrays of copies of each of a large number of genes are bound to small glass slides so they can be used to quantify the amounts of their ribonucleic acids (RNA) produced under differing conditions. For example, RNA can be isolated from plants both infected and not infected with a pathogenic fungus so that the genes that are turned on in response to the fungus can be rapidly identified. These and many other similarly large-scale analyses will allow swift determination of how plants respond to their environment and the full set of changes that occur in different stages of development.

Monocots

The monocotyledons (or, in abbreviated form, the monocots), class Liliopsida, are one of the major groups of flowering plants (angiosperms). There are about 100 families and 67,000 species of monocots, and the monocots consequently represent about one-fourth of the approximately 250,000 species of flowering plants. Some of the larger families of monocots are the grass family (Poaceae, or Gramineae), palm family (Arecaceae, or Palmae), and orchid family (Orchidaceae).

Economic and Ecologic Importance

Many of the most important plant species grown for human consumption are in the grass family, which includes rice, corn (maize), wheat, rye, barley, teff, millet, and other species. Many species of the grass family are also grown for animal consumption or as lawn grasses; examples include timothy, fescue, and bluegrass. Another group of great economic importance is the palm family, which includes coconuts, dates, and the oil palm. In addition to these foods, the palm family provides construction materials for housing, thatching, and a variety of tools and implements in many parts of the world. The largest family of monocots, in terms of number of species, is the orchid family. Although orchids are widely grown as ornamentals, only one species, the vanilla orchid, is grown as a food plant. The flavoring agent vanilla is extracted from the podlike fruits of this species.

Apart from their obvious economic importance as sources of foods and other materials of use to humanity, various monocots are of great significance as dominant elements in a variety of habitats, such as prairies (many grasses), marshes, bogs, and other wetlands (many members of the sedge family, or Cyperaceae), and ponds and streams (various members of the frog's-bit family, Hydrocharitaceae, and related aquatic families). Members of the orchid family and the pineapple family (Bromeliaceae) are important **epiphytes** in tropical forests, where they provide food to pollinating insects and birds and habitat for insects, fungi, and other kinds of organisms in the forest canopy.

epiphytes plants that grow on other plants

Anatomy

One of the distinctive characteristics of monocotyledons is the feature that gives the group its name, the presence of a single cotyledon, or seed leaf, in the embryo (as opposed to two in dicotyledons). Another important characteristic of monocots is the early death of its primary root, the initial root that emerges when a seed germinates. Thus, there is no taproot, and the entire root system of an older plant consists entirely of roots that emerged from stems. Another characteristic of monocots is the presence of scattered **vascular** bundles in the stems, as observed in cross-section, in contrast with the characteristic arrangement of the vascular bundles in a ring, as occurs in dicots and **gymnosperms**. Secondary growth, the process by which a stem or root continues to increase in girth through the development of additional cell layers, occurs in only a few monocots, such as the Dracaena. True wood (as occurs in gymnosperms and many dicots) is the result of secondary growth, and because this form of development is absent in most monocots, almost all of them are herbaceous plants.

vascular related to transport of nutrients

gymnosperm a major group of plants that includes the conifers

COMMON MONOCOT FAMILIES

Family	Common Name	Number of Species (approximate)	Uses
Araceae	Aroid family	3,300	Taro and other species cultivated for starchy tubers and rhizomes; many ornamentals
Arecaceae (or Palmae)	Palm family	2,000	Food (dates, coconuts, oil); construction of houses; numerous implements such as baskets
Bromeliaceae	Bromeliad family	2,700	Pineapples; ornamentals
Cyperaceae	Sedge family	5,000	Ecological dominants in wetlands, providing habitat and food for wildlife
Hydrocharitaceae	Frog's-bit family	75	Habitat and food for aquatic animals; several species are noxious weeds in ponds; some species grown in aquaria or ponds as ornamentals
Liliaceae	Lily family	600	Lilies, tulips, and other ornamentals
Orchidaceae	Orchid family	25,000	Vanilla; numerous ornamentals
Poaceae (or Gramineae)	Grass family	11,000	Grain for human consumption and both grain and vegetation for animal consumption; ecological dominants in prairies and other ecosystems; lawn grasses; bamboos
Zingiberaceae	Ginger family	1,400	Ginger, turmeric, and other spices; ornamentals

Monocots nonetheless exhibit a variety of growth forms. Most are perennial herbs, often with specialized organs such as bulbs, corms, tubers, and rhizomes, which store food resources. These structures, which are specialized stems with or without specialized leaves, are seen in many perennial herbs such as crocuses, daffodils, irises, and onions. The aboveground parts of these plants die back each year when a cold or dry season approaches and are regenerated from the various belowground structures when suitable growing conditions return. Although they are often called trees, banana plants are actually large herbaceous perennials that lack wood as well as a vertical trunk. The actual stem of a banana plant extends only a short distance above the base of the plant, and what appears superficially to be the main stem is actually a tight aggregation of the lower parts of the leaves. Most monocots that are woody in texture, such as bamboos and palm trees, lack secondary growth, and their stems are relatively uniform in diameter from the base to the top of the plant. Several families of monocots are floating or rooted aquatics in fresh and salt water. These plants often have ribbonlike stems and leaves, and can be mistaken for algae if their flowers and fruits are overlooked.

Many species of monocots have leaf bases that completely encircle the stem, thus forming a sheath. The layers of an onion bulb (members of the Alliaceae family) are leaves of this type. In the leaf blades of most monocots the major strands of vascular tissue (the veins) are parallel to each other. In this manner they differ from the typically reticulate or netlike system of veins that occurs in most dicots, where the major veins branch and diverge, with many of the branches meeting. There are exceptions, and a reticulate leaf venation system occurs in some groups of monocots, such as the aroid family (Araceae), which includes skunk cabbage, Jack-in-the-pulpit, and philodendron, the latter of which is frequently grown as a houseplant. An unusual variant form of parallel leaf venation occurs in a group of monocots that includes the ginger family (Zingiberaceae) and the banana family

(Musaceae). In these families, as exemplified by the leaf of the banana plant, there is a bundle of parallel veins along the midrib of the leaf, and these diverge in succession toward the margin of the leaf, the result being a characteristic pinnate-parallel leaf venation pattern.

In most monocots, the floral parts occur in multiples of three. One example is the tulip, which has six petals (often called tepals, since there is no clear differentiation of **sepals** and petals), six stamens, and a **pistil** with three chambers or locules, representing the three **carpels**. The pollen grains of monocots also differ from those of most dicots. In monocots, each pollen grain has just one thin-walled region, the colpus, which is the area from which the pollen tube emerges when the pollen grain germinates. Most dicots, in contrast, have three such regions. This thin area of the pollen wall often takes the form of a single elongate furrow, or sulcus, that extends most of the length of the pollen grain. SEE ALSO ALLIACEAE; BAMBOO; DICOTS; EVOLUTION OF PLANTS; GRASSES; ORCHIDACEAE; PALMS; SYSTEMATICS, PLANT.

Jerrold I. Davis

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

pistil the female reproductive organ

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

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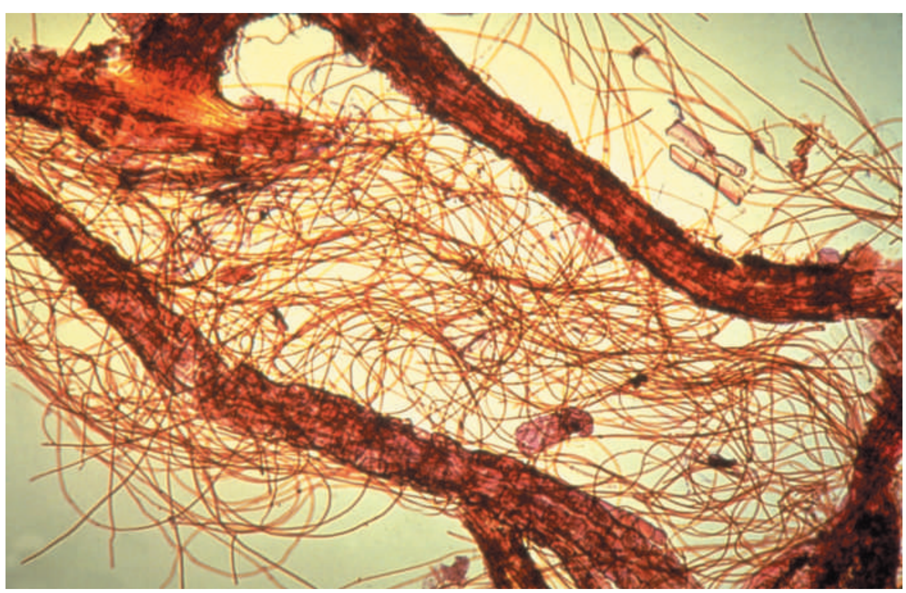
Mushroom *See Fungi.*

Mycorrhizae

Mycorrhizae are intimate, mutually beneficial associations between fungi and the roots of plants (*mycorrhiza* comes from the Greek word meaning "fungus-root"). All **gymnosperms** and approximately 80 percent of all an-

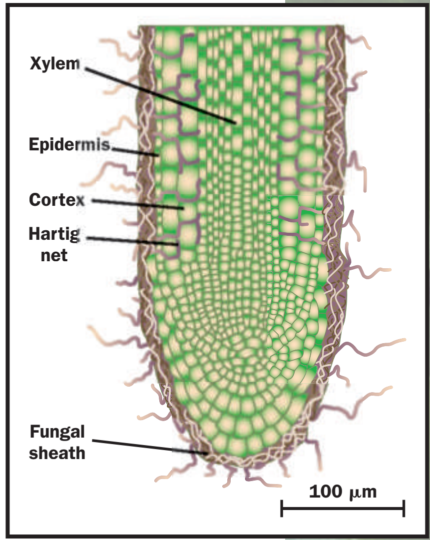
gymnosperm a major group of plants that includes the conifers



Ectotrophic mycorrhizae on host roots.

giosperms are thought to have naturally occurring mycorrhizal associations. The plant provides the fungus with carbohydrates made in photosynthesis, and the fungus provides the plant with increased amounts of mineral elements and water absorbed from the soil. The fungus also protects the root from **pathogens**.

There are two major types of mycorrhizae, the ectomycorrhizae (also called ectotropic mycorrhizae; *ecto*, meaning "outside") and the endomycorrhizae (endotropic mycorrhizae; *endo*, meaning "inside"), that are distinguished on the basis of whether or not the fungus penetrates the root cells.



Ectotrophic mycorrhizal fungi infecting a root. Redrawn from Taiz and Zeiger, 1998, Figure 5.10.

pathogen disease-causing organism

Ectomycorrhizae

In ectomycorrhizae the fungal component is usually a basidiomycete or sometimes an ascomycete. Ectomycorrhizae occur on certain groups of temperate shrubs and trees such as beeches, oaks, willows, poplars, cottonwoods, and pines. The associations are most common in vegetation experiencing seasonal growth, where they are thought to extend the growing period. In addition, ectomycorrhizae are common on trees growing in the cold, dry conditions close to the Arctic Circle and high on the slopes of mountains where they make the trees better able to survive in harsh conditions.

In an ectomycorrhizal association, the fungus forms a thick mat, called a mantle, on the outside of the young roots, and it also grows in between epidermal cells and into the cortex of the root interior. Within the root, the fungus never penetrates any of the cells but instead remains confined to the intercellular spaces where it forms a network called a Hartig net. The fungal **filaments**, called **hyphae**, also extend outward from the root where they increase the volume of soil available to be "mined" for nutrients. They also increase the surface area for the absorption of water and mineral salts, particularly phosphates but also NH_4, K^+, Cu^{2+}, Zn^{2+}, and NO_3^-. Once the root is colonized by the fungus, the production of root hairs slows or even ceases as the absorptive role of the root hairs is taken over by the hyphae of the ectomycorrhizal fungus.

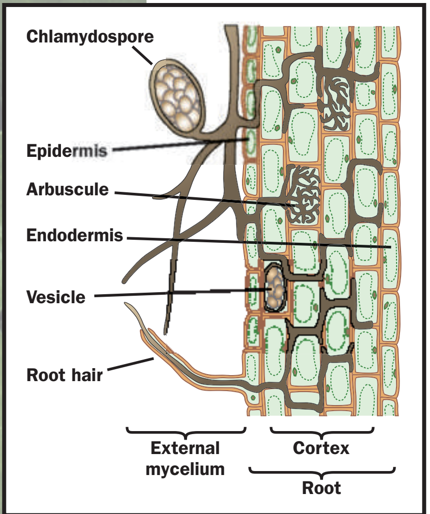
filament a threadlike extension

hyphae the threadlike body mass of a fungus

Endomycorrhizae

Far more common are the endomycorrhizae, which have a zygomycete as the fungal component and which actually penetrate the cell walls of the root cortex. Although the hyphae do not enter the cytoplasm of the **cortical** cells, in most cases they cause the plasma membrane to bulge inward, forming highly branched structures called arbuscules and terminal swellings called vesicles. Thus, this type of endomycorrhizae is referred to as vesicular-arbuscular mycorrhizae, or VAM. The arbuscules are in intimate contact with the cortical cells and provide an increased surface area over which carbohydrates can pass from the plant to the fungus and mineral elements from the fungus to the plant. The vesicles are thought to function as storage compartments for the fungus. As with the ectomycorrhizae, the fungal hyphae extend from the root into the soil and increase the surface area for absorption, but there is no mantle or Hartig net, and root hairs are often present. The VAM are found on almost all herbaceous angiosperms, some gymnosperms, and many ferns and mosses. Endomycorrhizae are particularly important in the tropics where the soils are typically poor in phosphates. Studies have indicated that roots associated with

cortical relating to the cortex of a plant



Association of vesicular-arbuscular mycorrhizal fungi with a plant root section. Redrawn from Taiz and Zeiger, 1998, Figure 5.11.

enzyme a protein that controls a reaction in a cell

compound a substance formed from two or more elements

ecosystem an ecological community together with its environment

mycorrhizal fungi can take up phosphate four times faster than roots without such fungi. Mycorrhizal fungi are particularly effective in utilizing highly insoluble rock phosphorus, $Ca_3(PO_4)_2$, that cannot be used by plants. The fungal hyphae make phosphates available to the plant by converting them to a soluble form.

Other Associations

Two other types of mycorrhizae are found in the heather and orchid families. In heather (family Ericaceae), the fungus secretes **enzymes** into the soil that convert materials, particularly nitrogen-containing **compounds**, into forms that can be taken up more readily. In orchids (family Orchidaceae), the seeds contain a mycorrhizal fungus that is required for seed germination. Within the seed, the hyphae absorb stored carbohydrates and transfer them to the plant embryo.

Some plants, such as those of the mustard family (Brassicaceae) and the sedge family (Cyperaceae), lack mycorrhizae. In addition, most plants growing in flooded soils (or under hydroponics) do not form mycorrhizae nor do plants grown where conditions are extremely dry or saline. Also, plants growing in very fertile (i.e., nutrient-rich soils) have less-developed mycorrhizae compared to plants growing in nutrient-poor soils.

Ecological Importance of Mycorrhizae

The importance of mycorrhizae in **ecosystems** became particularly apparent in the 1960s when plants grown in greenhouses were transplanted into areas such as slag heaps, landfills, and strip-mined areas in order to reclaim the land. With few exceptions, such plants did not survive in these infertile areas. Not until later was it realized that greenhouse soil is often sterilized to prevent the growth of pathogens, and the sterilization process killed the mycorrhizal fungi as well. Today, such reclamation attempts are much more successful because mycorrhizal fungi are inoculated with the plants when they are transplanted into the reclaimed areas. Similarly, attempts to grow certain species of European pines in the United States were unsuccessful until mycorrhizal fungi from their native soils were added at the time of transplanting.

Mycorrhizae are thought to have played an important role in the colonization of the land by plants some four hundred million years ago. Studies of fossil plants have shown that endomycorrhizae were prevalent at that time, and such associations may have been crucial in helping plants make the transition from the nutrient-rich sea to the nutrient-poor land. SEE ALSO Ecosystem; Fungi; Interactions, Plant-Fungal; Nutrients.

Robert C. Evans

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Native Food Crops

Native food crops are the crops of the world's ancient farming systems. The seeds of these cultivars have been passed down by native agriculturalists across generations and selected and preserved for local **ecosystems**. Native seeds, and the methods used to grow them, were developed for a wide range of temperatures, soil types, and precipitation without expensive, often ecologically destructive, chemicals. Many of these crops continue to be grown around the world today by traditional, indigenous farmers. They represent irreplaceable sources of genetic material to improve modern **hybrid** crops for nutrition as well as for disease and drought resistance. Examples of modern food crops that had their origin from native sources include corn, rice, chilies, potatoes, and wheat. Other highly nutritious crops such as quinoa and amaranth are becoming more common in Western diets, while ulloco (oo-yoo-ko), a wildly colored, high-altitude tuber (root crop) that was a staple of the Incas, is still relatively unknown outside of South America. SEE ALSO AGRICULTURE, HISTORY OF; BARK; CULTIVAR; ETHNOBOTANY; SEED PRESERVATION; SEEDS.

Miguel L. Vasquez

ecosystem an ecological community together with its environment

hybrid a mix of two species

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Nitrogen Fixation

Biological nitrogen (N_2) fixation is the reduction of atmospheric nitrogen gas to ammonia, according to the equation:

$$N_2 + 10H^+ + 8e^- + 16ATP \rightarrow 2NH_4^+ + H_2 + 16ADP + 16P_i$$

The reaction is mediated by an oxygen-sensitive **enzyme** nitrogenase and requires energy, as indicated by the consumption of adenosine triphosphate (**ATP**). This conversion of **inert** N_2 gas into a form utilized by most organisms is the second most important biological process on Earth after photosynthesis. It contributes 175 million tons of nitrogen per year to the global nitrogen economy and accounts for 65 percent of the nitrogen used in agriculture. In Brazil alone, N_2 fixation contributes the equivalent of 2.5 million tons of fertilizer nitrogen annually to agricultural production and is essential to a country with limited natural gas reserves for fertilizer nitrogen production.

This article emphasizes **symbiotic** N_2 fixation in grain and pasture **legumes** in the family Fabaceae. N_2 fixation also occurs in leguminous and actinorhizal trees, sugarcane, and rice.

N_2-Fixing Organisms and Variation in Their Rates of Fixation

The ability to fix N_2 is restricted to prokaryotic organisms. Within this group the ability occurs in many different species. These include **cyanobacteria** and **actinomycetes,** as well as eubacteria, including heterotrophic (e.g., *Azotobacter*), **autotrophic** (*Thiobacillus*), aerobic (*Bacillus*), **anaerobic** (*Clostridium*), and photosynthetic (*Rhodospirillum*) species.

enzyme a protein that controls a reaction in a cell

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

inert incapable of reaction

symbiosis a relationship between two organisms from which each derives benefit

legumes beans and other members of the Fabaceae family

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

actinomycetes common name for a group of Gram positive bacteria that are filamentous and superficially similar to fungi

autotroph "self-feeder;" any organism that uses sunlight or chemical energy

anaerobic absence of oxygen

Root nodules of the broad bean *Vicia faba* formed by the nitrogen-fixing bacteria *Rhizobium.*

symbiosis a relationship between organisms of two different species in which at least one benefits

N_2-fixing organisms can live free in nature (e.g., *Azotobacter*), enter loose (associative) **symbiosis** with plants or animals (*Acetobacter* and sugarcane), or establish longer-term relationships within specialized structures provided by their host (*Rhizobium* and the legume nodule).

Some free-living organisms fix enough N_2 in vitro to grow without added nitrogen, but limited energy supply can limit N_2 fixation in nature. For instance, non-symbiotic organisms in primary successional areas of the Hawaii Volcanoes National Park were found to fix only 0.3 to 2.8 kilograms of N_2 per hectare per year, and non-symbiotic N_2 fixation in soil rarely exceeds 15 kilograms per hectare per year. Higher levels in tidal flats and rice paddies are largely due to photosynthetic bacteria and cyanobacteria.

The importance of energy supply for fixation can be seen by comparing these rates to those found in legumes, where the symbiotic bacteria are supplied with high-energy products from photosynthesis. Rates of symbiotic N_2 fixation in legumes vary with plant species and cultivar, growing season, and soil fertility. Some forage legumes can fix 600 kilograms per hectare per year but more common values are 100 to 300 kilograms per hectare per year. Rates for grain legumes are often lower. Inclusion of legumes in **crop rotations** is generally thought to improve soil nitrogen levels, but benefits depend on the level of N_2 fixed and the amount of nitrogen removed in grain or forage. A good soybean crop might fix 180 kilograms per hectare but remove 210 kilograms per hectare in the grain.

crop rotation alternating crops from year to year in a particular field

Nodule Formation and Structure in Legumes

The most-studied symbiotic system is between N_2-fixing bacteria known as rhizobia and legumes such as clover and soybean. Rhizobia produce stem or root nodules on their host(s), and within these nodules receive protection from external stresses and energy for growth and N_2 fixation. The host receives most of the nitrogen it needs for growth. Six genera of rhizobia (*Rhizobium*, *Azorhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Sinorhizobium*, and *Allorhizobium*) are recognized.

Rhizobia use several different mechanisms to infect their host, but only infection via root hairs is described here. Infection is initiated with the attachment of suitable rhizobia to newly emerged root hairs and leads to localized hydrolysis of the root hair cell wall. Root hair curling and deformation results, with many of the root hairs taking the shape of a shepherd's crook. Hydrolysis of the cell wall allows rhizobia to enter their host, but they never really gain intracellular access. Plant-derived material is deposited about them, and as they move down the root hair toward the root cortex they remain enclosed within a plant-derived infection thread. Even within the nodule they are separated from their host by a host-derived **peribacteroid** membrane. This separation is usually seen as a mechanism to suppress plant defense responses likely to harm the bacteria.

peribacteroid a membrane surrounding individual or groups of rhizobia within the root cells of their host; in such situations the bacteria have frequently undergone some change in surface chemistry and are referred to as bacteroids

Presence of the rhizobia causes multiplication and enlargement of root **cortical** cells and gives the nodule a characteristic shape and structure: either round as in soybean or elongated as in alfalfa or clover. Such nodules have several distinct regions. The area of active N_2 fixation is either pink or red in color due to the presence of hemoglobin needed for oxygen transport. In most legumes nodules are visible within six to ten days of **inoculation;** N_2 fixation as evidenced by improved plant growth and coloration of the nodules can occur within three weeks.

cortical relating to the cortex of a plant

inoculation use of a commercial preparation, most often but not always peat-based, used to introduce rhizobia into soils; inoculants may be seed applied or introduced directly into the soil

Molecular Changes Associated with Nodulation and N_2 Fixation

The signs of infection are paralleled at a molecular level by signaling between host and rhizobia. Nodulation genes in *Rhizobium* are borne on extra-chromosomal (plasmid) deoxyribonucleic acid (DNA). They include both common genes found in all rhizobia and host-specific genes involved in the nodulation of specific legumes. Most are only expressed in the presence of a suitable host. Substances termed **flavonoids** present in the root exudate trigger this response, with legumes differing in the flavonoids each produced. Rhizobia also differ in their response to these **compounds**.

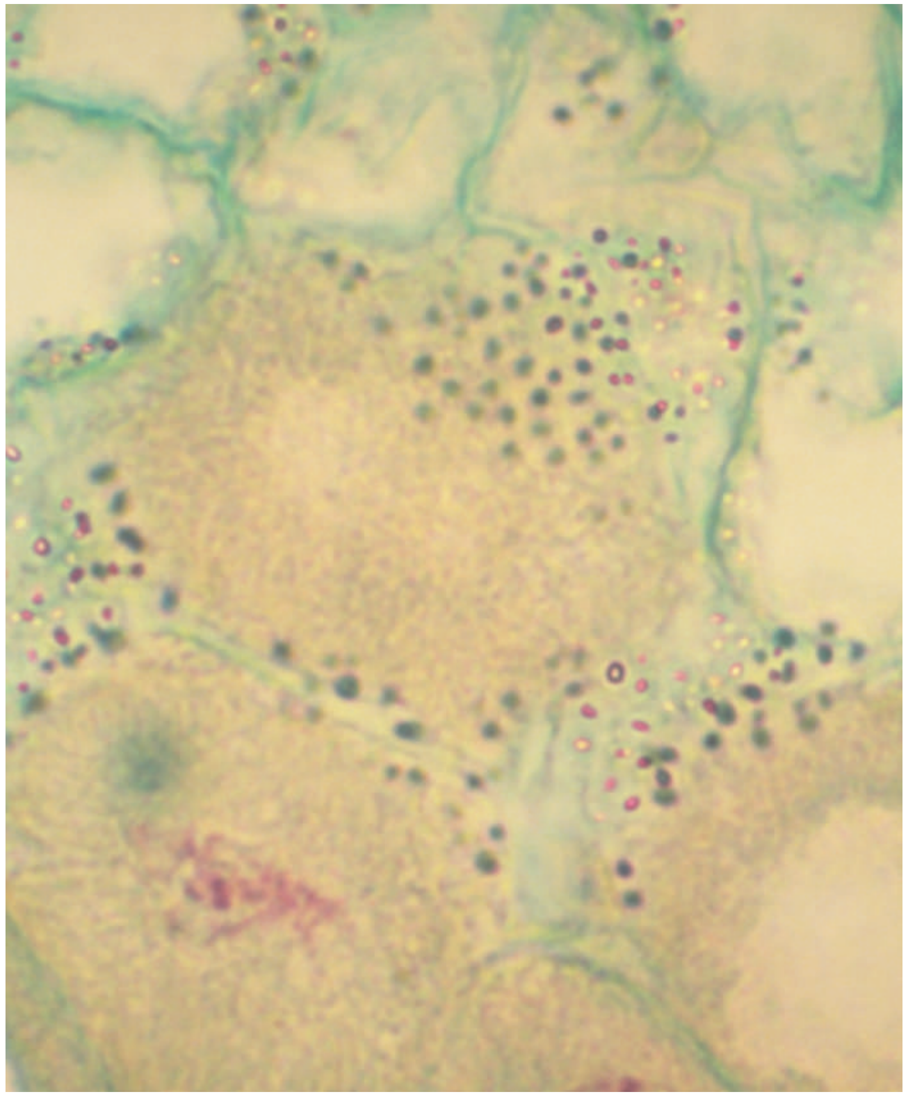
flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

compound a substance formed from two or more elements

More than fifty nodulation genes have been identified. Some are involved in the regulation of nodulation, but most function in the synthesis of a **chitin**-like lipo-chito-oligosaccharide or nod factor. These molecules all have the same core structure (coded for by the common nodulation genes), but they vary in the side chains each carries, affecting host range.

chitin a cellulose-like molecule

A micrograph of *Rhizobium* in the root of a bean plant.



They are powerful plant hormones, which at low concentration can initiate most of the changes found during nodule development.

Interaction of host and rhizobia is also accompanied by the expression of nodule-specific proteins or nodulins. Several nodulins have now been found in actinorhizal and mycorrhizal symbiosis, and together with pea mutants that neither nodulate nor form mycorrhizal associations indicate some common elements in symbiosis.

Nodulin expression can vary temporally and spatially. Early nodulins are involved in infection or nodule development and may be expressed within six hours of inoculation. Later nodulins are involved in nodule function, carbon and nitrogen metabolism, or to O_2 transport. Nodule hemoglobin is an obvious example of this group.

Specificity in Nodulation

Given the complex signaling involved, specificity in nodulation is to be expected. Each rhizobium has the ability to nodulate some, but not all, legumes. Host range can vary, with one rhizobia only nodulating a particular species of clover, for example, while another will nodulate many different legumes. A consequence of this specificity is that legumes being introduced into new areas will usually need to be inoculated with appropriate rhizobia before seeding. In the early 1900s this was often achieved by mixing seed with soil from an area where the crop had been grown before. Today, more than one hundred different inoculant preparations are needed for the different crop, tree, and pasture legumes used in agriculture and conservation. Most are grown in culture and sold commercially. The legumes for which inoculant preparations are available, and the methods used to prepare, distribute, and apply these cultures, are detailed on the Rhizobium Research Laboratory Web site (http://www.Rhizobium.umn.edu).

When properly carried out, legume inoculation should result in abundant nodulation and high levels of N_2 fixation. Reinoculation should not be necessary because large numbers of rhizobia will be released from nodules at the end of the growing season and establish themselves in the soil. Problems with the culture used and environmental and soil factors can limit response, especially in the lesser-developed countries. Common concerns include:

- poor-quality inoculant strains weak in N_2 fixation and noncompetitive or nonpersistent in soil
- inoculants with low rhizobial numbers because of problems in production or packaging or during shipment
- inappropriate use of fertilizer or pesticides injurious to the rhizobia
- soil acidity, drought, or temperature conditions that affect strain survival or nodulation and N_2 fixation.

Because of earlier problems in inoculant production and quality, many countries have now developed regulations governing the quality of inoculant cultures. In the United States, inoculant quality control still rests with the producer. SEE ALSO Atmosphere and Plants; Biogeochemical Cycles; Cyanobacteria; Eubacteria; Fabaceae; Fertilizer; Flavonoids; Mycorrhizae; Nutrients; Roots.

Peter H. Graham

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Nutrients

Of the ninety-two naturally occurring elements, only about twenty are indispensable or essential for the growth of plants. Plants, however, absorb many more mineral elements than that from the soil in which they grow. Which of these elements are the essential ones? The best way to answer that is to withhold the element in question from the plants. If then the plants grow poorly or die while plants supplied with the element thrive, the element has been shown to be essential.

A Swiss cheese plant (*Montsera,* family Araceae), suffering from marginal chlorosis, indicating a nitrogen deficiency.

Such an experiment cannot be done with soil-grown plants. Soils contain most of the elements in the periodic table of elements. No element can be removed from soil so thoroughly as to deprive plants of that element; the chemical means for doing that would destroy the soil.

Therefore scientists devised a simplified method for growing plants, called solution culture, or hydroponics. In this technique the roots of the plants are not in soil but in water, which contains the dissolved salts of those elements considered to be essential. That way, scientists can control and monitor the chemical composition of the medium in which the plants grow.

Failure of the plants in such an experiment suggests that some essential element is missing, and by trial and error scientists then determine which element cures the deficiency. By this method most of the elements known now to be essential have been identified. Those elements needed in relatively large amounts are called macronutrients; those needed in only small or very small amounts are micronutrients.

By the latter half of the nineteenth century, all the macronutrient mineral elements (see accompanying table) and one micronutrient, iron, had been identified. But throughout the twentieth century additional elements were shown to be micronutrients. It took so long to identify them because early on the water and the nutrient salts used for supplying the macronutrient elements contained substantial impurities, some of which were micronutrients. Investigators therefore supplied, without knowing it, several micronutrients

MINERAL ELEMENTS IN CROP PLANTS

Element	Range of Concentrations
Macronutrients	
Nitrogen (N)	0.5–6%*
Phosphorus (P)	0.15–0.5%
Sulfur (S)	0.1–1.5%
Potassium (K)	0.8–8%
Calcium (Ca)	0.1–6%
Magnesium (Mg)	0.05–1%
Micronutients	
Iron (Fe)	20–600 ppm†
Manganese (Mn)	10–600 ppm
Zinc (Zn)	10–250 ppm
Copper (Cu)	2–50 ppm
Molybdenum (Mo)	0.1–10 ppm
Chlorine (Cl)	10–80,000 ppm
Boron (B)	0.2–800 ppm
Nickel (Ni)	0.05–5 ppm
Other Elements	
Sodium (Na; essential for some plants)	0.001–8%
Silicon (Si; quasi-essential for some plants)	0.1–10%
Cobalt (Co; essential in all nitrogen-fixing systems)	0.05–10 ppm

* Percent of dry matter.
† Micrograms per gram dry matter (or parts per million).

SOURCE: Data collected from various sources.

to their experimental plants. Once this was understood, plant biologists developed ever more refined methods for purifying water and nutrient salts and, little by little, several additional elements were shown to be essential.

When determining the chemical composition of plants, plant nutritionists usually dry the plant first, keeping it at about 70°C (158°F) for forty-eight hours. Fresh plant material is mostly water (H_2O) so that its dry weight is only around 10 to 20 percent of the initial fresh weight. Carbon and oxygen each make up about 45 percent of the dry matter, and hydrogen 6 percent. These elements can be removed by careful digestion. The inorganic nutrients together make up only about 4 percent of dry plant matter and are left in the digest.

Essential Elements

The table above lists the elements known to be essential to plants, in addition to carbon, oxygen, and hydrogen, and also includes a quantitative indication of their prevalence in plant tissues. For the macronutrient elements, these values are expressed as percent of the dry matter, and for the micronutrients, as micrograms per gram dry matter, or parts per million. The reason for giving a range of values rather than a single one for each element is that these values differ considerably, depending on the kind of plant, the soil in which it grows, and other factors. Three of these elements, sodium, silicon, and cobalt, cannot unequivocally be called nutrients, as explained below.

Living plants use up much water in **transpiration**. Water is also their main constituent. Carbon, oxygen, and hydrogen are the elements that make up carbohydrates. Plant cells have walls composed mostly of cellulose and related carbohydrate polymers. These three elements make up a high per-

transpiration movement of water from soil to atmosphere through a plant centage of plant dry matter because quantitatively most of it is cell wall. In addition, it is mainly in the form of sugars (i.e., carbohydrates) that carbon initially assimilated by leaves through photosynthesis is **translocated** to the rest of the plant body, including the roots.

translocate to move, especially to move sugars from the leaf to other parts of the plant

compound a substance formed from two or more elements

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

enzyme a protein that controls a reaction in a cell

solute a substance dissolved in a solution

symbiosis a relationship between two organisms from which each derives benefit

legumes beans and other members of the Fabaceae family

- **Nitrogen** is a component of all amino acids, and as proteins are amino acid polymers, of all proteins. Nucleic acids and other essential **compounds** also contain nitrogen.
- **Phosphorus** is part of several compounds essential for energy transfer, of which adenosine triphosphate (**ATP**), the "energy currency" of cells, is the best known. Nucleic acids and several other classes of biochemical entities also contain phosphorus as an integral component.
- Three **sulfur**-containing amino acids and other compounds needed in metabolism account for the essentiality of sulfur.
- **Potassium** is not an integral part of any compound that can be chemically isolated from plants. However, it activates some seventy **enzymes**, and along with other **solutes** regulates the water relations of plants.
- **Calcium** is part of the middle lamella, the layer between the cell walls of adjacent cells. Another function is maintenance of the integrity of cell membranes. Calcium is also a cofactor (nonprotein part) of several enzymes. It functions to signal environmental changes in plant cells.
- **Magnesium** is a constituent of the chlorophyll molecule and activates numerous enzymes.
- **Iron** is a part of many metabolites, including those primarily involved in energy acquisition (photosynthesis), utilization (respiration), and nitrogen fixation.
- **Manganese** activates a number of enzymes and is part of the protein complex that causes the evolution of oxygen, O_2, in Photosystem II of photosynthesis.
- **Zinc** is a constituent of several enzymes.
- **Copper** is also a constituent of several enzymes.
- **Nickel,** the element required in the least amount, is a constituent of the enzyme urease. A deficiency of it causes an excessive accumulation of urea.
- **Boron** has several functions in plant growth; severe boron deficiency causes the growing tips of both roots and shoots to die.
- **Chlorine** (in the form of chloride ion) is required in Photosystem II of photosynthesis. Severely chlorine-deficient plants wilt, suggesting some unknown function in water relations.
- **Molybdenum** is a constituent of enzymes active in the acquisition of nitrogen.
- **Cobalt** is required by the **symbiotic** nitrogen-fixing bacteria associated with the root nodules of **legumes** and some other plants.
- **Sodium** is prominent in many soils of arid and semiarid regions, and native wild plants growing on these saline soils grow best with an ample supply of it. Crops, however, often suffer under saline con-

ditions. Plants with the C_4 photosynthetic pathway require sodium as a micronutrient.

- **Silicon** is essential for plants of the family Equisetaceae, the horsetails or scouring rushes. Although apparently not absolutely essential for plants in general it has nevertheless many beneficial effects; it has been called quasi-essential.

Deficiency and Toxicity Symptoms

When some element is deficient or present in such high concentration as to be toxic, plants often have symptoms somewhat characteristic of the particular condition afflicting them. For example, yellowing of leaves, or chlorosis, often indicates a deficiency of nitrogen. Nevertheless, visual identification of deficiencies or toxicities is not a reliable procedure. For example, sulfur deficiency may result in symptoms very similar to those of nitrogen deficiency. Therefore even experts check their visual impression by analyzing the tissue to find out whether its content of the suspected element is in fact below the value deemed adequate for that particular crop or present in excess. Often, such unrelated conditions as diseases caused by fungi or bacteria may result in the development of symptoms that mimic those of nutrient disorders. SEE ALSO Biogeochemical Cycles; Fertilizer; Halophytes; Hydroponics; Nitrogen Fixation; Soil, Chemistry of.

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Odum, Eugene

O

American Ecologist
1913–

Eugene Odum is an American ecologist who has worked to advance ecological awareness and research. Born in 1913 to an academic family, he spent most of the twentieth century promoting the ecosystem concept and warning of the impact humans have on the **ecosystems** in which we live. One of his most important accomplishments was writing *Fundamentals of Ecology* in 1953, which he wrote partly in response to the zoology department at the University of Georgia rejecting ecology as an important area of study. His book was remarkably clear and concise, and it presented the important principles of ecology in a way that helped to define the science.

ecosystem an ecological community together with its environment

Fundamentals of Ecology also brought the idea of an ecosystem to a wider audience at a time when the concept was just beginning to gain recognition among ecological specialists and ways to study ecosystems were just being developed. Previously, ecology had focused on natural history and on the variety of species in the environment rather than on the details of physical and metabolic interactions among the species and nonliving material around them, as is done in the study of ecosystems. Odum placed the idea of the ecosystem at the beginning, as a fundamental concept of ecology. He explained that ecosystems are the largest functional unit in ecology, comprising both living and nonliving parts that exchange materials in cycles. These interactions and exchanges of nutrients could allow ecosystems to evolve as units over time. Ecosystems could be seen at many levels, from something as small as a lake to the entire Earth seen as a global ecosystem.

In emphasizing how the study of ecology needs to examine the way humans affect their ecosystems, Odum published ideas that became the focus of the environmental movement. Given the knowledge that humans were influential and often destructive components of ecosystems, it was especially important that Odum's book was clear and understandable by non-ecologists. Being at the time one of the only ecological textbooks, *Fundamentals of Ecology* was enormously important in driving the study of ecosystems.

Odum also wrote several other works while teaching and doing research at the University of Georgia. His work was funded by the Atomic Energy Commission, an institution that funded much early ecological research. He became a leading authority on ecosystem studies, defending the new discipline against its critics, and he also served as chair of a section of the International Biological Program. His leadership in the program helped guide research into landscape ecosystems, studying terrestrial and marine areas and the human influences on them. Remaining active into his late eighties by the turn of the twenty-first century, Eugene Odum still worked to promote the study of ecosystems. He has done much to encourage environmental study around the world, and especially where he works in Georgia. SEE ALSO ECOLOGY; ECOLOGY, ENERGY FLOW; ECOLOGY, HISTORY OF; ECOSYSTEM; WARMING, JOHANNES.

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Oils, Plant-Derived

Plant oil sources are typically the seeds or seed coats of plants. Plant breeding and genetic engineering have made available many plant oils with fatty acid compositions quite different from the typical values cited in the accompanying table.

Oils are extracted from plants by using pressure or solvents, usually the petroleum fraction hexane. Olive oil, for example, is a typical seed coat oil and is extracted by multiple pressings of the fruit pulp. The oil from the first pressing has the best quality and is termed virgin oil. Oilseeds may be extracted with pressure in a mechanical expeller but usually are cracked and pressed into flakes for extraction with hexane. The hexane is removed from the extracted crude oil by distillation.

Crude oils contain small amounts of undesirable **pigments**, phospholipids, and free fatty acids (i.e., fatty acids not chemically linked to glycerol) that make the oils dark, hazy, and smoky, respectively, on heating. Olive oil has a good flavor and is typically sold without treatment other than filtering or **centrifugation** for clarity. However, most other oils are refined. Refining involves mixing with water to wash out phospholipids (degumming), treatment with lye solutions to remove free fatty acids, bleaching with absorptive clays to remove pigments, and a vacuum steam treatment (deodorization) to remove undesirable flavors. Plant oils also contain small amounts of **sterols** and fat-soluble vitamins. These may be partly removed by deodorization and are regarded as harmless or desirable components of the oil.

Although most plant oils are used as food they are also used to make such things as paint and surface coatings, detergents, linoleum, and plastics. Some plant oils, such as castor and tung, contain special fatty acids used to make surface coatings.

Oils from plants are chiefly triglycerides, which are made up of one glycerol molecule linked to three fatty acids. The fatty acids have linear carbon chains varying in length, generally from six to twenty-two carbon atoms, with various amounts of hydrogen linked to the carbon. Carbon chains that hold all the hydrogen that they can are called saturated, and those with less hydrogen are unsaturated. Where the unsaturation occurs, the carbon chain is linked by double bonds.

Most plant oils are clear liquids at ambient temperatures rather than fats, which are plastic solids at room temperature. Butters, such as cocoa butter (chocolate fat), melt around room temperature. The solidification temperature of an oil depends on the length and saturation of its fatty acid chains. Short chains and double bonds (less saturated) decrease the solidification point. To change liquid oils, such as soybean oil, to a shortening or margarine, the oil is treated with hydrogen under pressure and a nickel catalyst. The resulting more saturated fat is said to be hydrogenated. During hydrogenation some of the double bonds are converted from their native cis form to trans isomers.

Fats and oils provide the most concentrated source of calories in the human diet, about nine calories per gram. Certain fatty acids produced in plants are nutritionally required. These essential fatty acids contain multiple double bonds and are called polyunsaturated. They come in two families called n-3 or n-6 based on the position of the first double bond counting from the tail of the fatty acid chain. SEE ALSO Economic Importance of Plants; Lipids; Seeds.

Earl G. Hammond

HEALTHY FATS AND OILS

Animal fats contain the sterol cholesterol. The human body naturally produces all the cholesterol it needs; therefore, overconsumption of fatty foods rich in cholesterol is believed to encourage artery disease. Artery disease is also influenced by the fatty acids we consume. Fats and oils are considered healthy if they contain low proportions of saturated fatty acids with chain lengths of twelve to sixteen carbons. The animal fats lard, tallow, and milk fat and the plant oils palm, palm kernel, and coconut contain significant proportions of these less-desirable fatty acids. An atherogenicitiy index (AI) for fats and oils has been proposed to predict their tendency to cause artery disease.

$$AI = [\%12{:}0 + 4\ (\%14{:}0) + \%16{:}0]\ /\ \%\ \text{all unsaturates}$$

where %12:0 represents the weight percent of a fatty acids with twelve carbons and no double bonds, and so on.

A low index value is desirable. The AI of animal fats range from 0.6 to 4. Some believe that consumption of the fatty acids with trans double bonds formed during hydrogenation also predisposes us to artery disease. Our diets should contain adequate amounts of the unsaturated n-3 and n-6 fatty acids. We should consume less than 30 percent of our total calories as fat.

pigments colored molecules

centrifugation spinning at high speed in a centrifuge to separate components

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sterol(s) chemicals related to steroid hormones

COMMON EDIBLE PLANT OILS

Oil Name	Plant Name	Oil-Bearing Tissue	Percentage C_{12}–C_{16} Saturated Fatty Acids*	Atherogenicity Index†
Canola	*Brassica campestris, Brassica napus*	Seed	6	0.04
Cocoa butter	*Theobroma cacao*	Seed	26	0.73
Coconut	*Cocos nucifera*	Seed	74	21.72
Corn	*Zea mays*	Seed	12	0.13
Cottonseed	*Gossypium hirsutum, Gossypium barbadense*	Seed	23	0.34
Olive	*Olea europea*	Seed coat	13	0.15
Palm	*Elaeis guineensis*	Seed coat	45	0.97
Palm kernel	*Elaeis guineensis*	Seed	73	7.12
Peanut	*Arachis hypogaea*	Seed	11	0.15
Safflower	*Carthamus tinctorius*	Seed	6	0.06
Sesame	*Sesamum indicum*	Seed	10	0.17
Soybean	*Glycine max*	Seed	11	0.13
Sunflower	*Helianthus annuus*	Seed	6	0.07

* Saturated fatty acids with 12 to 16 carbons are regarded as atherogenic or predisposing to artery disease.

† The atherogenicity index of Ulbrict and Southgate (1997) based on the data of Hammond (1991) is an estimate of the atherogenic effect of the various fatty acid. The smaller the index value, the more healthful the oil. Plant breeding and genetic engineering have made available many of these plant oils with fatty acid compositions greatly different from these typical values.

SOURCE: T. L. V. Ulbricht and D. A. T. Southgate, "Coronary Heart Disease: Seven Dietary Factors." *Lancet* 338 (1997): 985–92 and E. G. Hammond, "The Raw Materials of the Fats and Oils Industry." In *Fats and Oils Processing,* edited by P. Wan (Champaign, IL: American Oil Chemists' Society, 1991).

Opium Poppy

The opium poppy (*Papaver somniferum*) was known to humans before the time of the Greeks. In many cultures the plant has been considered an important medicine, used to treat pain and dysentery. The time and place of the origin of the opium poppy is a mystery. It probably arose in central Europe during the late Bronze Age and was taken southward into the Mediterranean region. It then spread eastward into the Orient, likely transported by Arab traders in the seventh century.

The opium poppy has been widely grown in southeast Asia, as well as in Afghanistan and Turkey. One of the most infamous areas of the world for opium poppies is the Golden Triangle, the region in southeast Asia where Burma, Laos, and Thailand meet. The poppy grows best at about 1,000 meters (3,300 feet) elevation. The fields are cleared by the slash-and-burn technique, in which the native plants are cut, dried, and burned in order to have a clear hillside for crops. The opium plant is an annual, and must be grown from seed each year. Often it is grown as a second crop during the rainy season, with the seeds being planted between maize (corn) plants in October, which provide protection to the young poppy seedlings. The maize is harvested and the old stems removed, allowing the poppies full sunlight and making it easier to weed. They grow to a height of about 1 meter (3 feet) in about three months. Flowers appear in December, varying in color from pure white to deep reddish-purple. The flower withers and the fruit, a capsule, begins to develop. In a week or so the capsule turns from green to slightly gray-green, and the latex is ready to harvest. The capsule is tapped with a special knife consisting of three to five razor-sharp blades, which cut fine slits in the fruit wall, allowing the milklike latex to ooze out. This latex contains the alkaloids for which the opium poppy is so well known. By the next day, it has congealed somewhat into a dark yellowish-brown mass, which is carefully scraped off and placed in a container. The dried latex is packaged and sold or further processed in a laboratory.

An opium poppy (*Papaver somniferum*) that was cut for its resin in a field in northwest Thailand.

Opium poppy latex contains more than twenty-five different alkaloids, of which six are important to humans. Morphine is a powerful painkiller, narcotic, and stimulant. It is strongly addicting but critical in modern medicine. Heroin is actually synthesized from morphine by the addition of two acetyl groups. It is a much stronger painkiller, but is also much more addicting. It is not used medically and has become a serious social problem because it has been badly abused. Papaverine, present in small amounts, is an important muscle relaxant. Codeine, the most extensively used opium alkaloid, is frequently found in cough medicines and decongestants. It is much less addicting than morphine or heroin, but may be sleep inducing. Narcotine speeds up respiration, but is used very little. Thebaine produces spasms similar to those caused by strychnine, and is sometimes used in the treatment of heroin addiction. SEE ALSO Alkaloids; Medicinal Plants; Psychoactive Plants.

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Orchidaceae

The plants belonging to the family Orchidaceae represent a pinnacle of evolutionary success in the plant kingdom. Represented by approximately twenty-five thousand species, they are possibly the largest family of flowering plants on Earth. Although orchids are most diverse in the tropics, they are found on every continent except Antarctica and can be found as far north as Alaska and as far south as Tierra del Fuego. Perhaps the main reason that orchids are so successful is that they have developed close relationships with insect pollinators and fungi. Their life histories are extremely complex and intricately woven together across three kingdoms of life: Plantae, Animalia, and Fungi.

Unlike other plants, orchid seeds contain no storage food for their **dormant** embryos. In order for most orchid seeds to germinate, they must be infected by fungal **hyphae**. After infection takes place, the orchid is able to take nourishment from the fungus, but it is unclear whether the fungus gets any benefit in return. This life strategy enables orchids to survive in habitats with poor soils, such as bogs, or those that lack soil altogether. Many tropical orchids are **epiphytes**, and some live completely underground, lacking chlorophyll and depending on fungi for all their nutritional needs.

dormant inactive, not growing

hyphae the threadlike body mass of a fungus

epiphytes plants that grow on other plants

The elaborate and intricate flowers of the *Paphiopedilum* orchid hybrid.

pistil the female reproductive organ

pheromone a chemical released by one organism to influence the behavior of another

The close association of orchids with insects was carefully studied by Charles Darwin. Through evolution, orchids have reduced their reproductive organs to one anther and one **pistil**. Moreover, orchids have fused these two organs into a single structure, the column, and have amassed all of their pollen into a single unit called a pollinium. As a consequence, most orchid flowers have only one chance to pollinate another flower. This strategy may seem risky, but when successful it delivers enough pollen to produce as many as seventy-two thousand seeds. To ensure success, orchids have evolved intricate pollination mechanisms. Some of these include explosive shotguns and glue to attach the pollinium to insects, or floral traps that force bees to take pollen with them when they escape. One of the most fascinating strategies is seen in orchids that not only mimic female wasps in morphology but also produce fragrances similar to female wasp **pheromones**. These orchids manage to fool male wasps into copulating with their flowers, thereby effecting pollination.

Only one orchid species, *Vanilla planifolia*, is of significant agricultural value, as the source of natural vanilla flavoring. Cultivation and processing of this spice is a long, labor-intensive process involving pollinating each flower by hand, drying and fermenting the fruits, and extracting the aromatic vanillin flavoring with alcohol. For this reason, natural vanilla is extremely expensive.

Vanilla, however, is not the only orchid of economic value. An enormous industry exists for cut flowers, corsages, and cultivation of orchids by hobbyists. Ancient texts indicate that orchids have been cultivated in China since at least 550 B.C.E. Today, the American Orchid Society alone has more than thirty thousand members, all of whom share a fascination and appreciation of these breathtakingly beautiful flowers. Unfortunately, many orchid species are threatened with extinction because of habitat destruction and over-collecting in the wild. However, all orchids are protected under international treaties. SEE ALSO Epiphytes; Horticulture; Interactions, Plant-Insect; Monocots; Pollination Biology.

Kenneth M. Cameron

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Ornamental Plants

Ornamental plants are grown for use by the green industry and public for purposes such as landscaping for sport, and conservation. The green industries include commercial plant nurseries, flower growers, parks, and roadside and landscape plant installation and maintenance.

The primary use for these plants is not for food, fuel, fiber, or medicine. However, ornamental plants contribute significantly to the quality of life by acting as barriers to wind, providing cooling shade, reducing or eliminating erosion, cleaning the air and water of pollutants including dust and chemicals, reducing noise pollution, and providing food and habitat for wildlife while making both suburban and urban areas more beautiful. Their economic and emotional impact is significant.

Ornamental plants include perennial deciduous and evergreen shade trees, conifers, and shrubs grown in horticultural production by the commercial nursery industry. Ornamental plants also include herbaceous and woody indoor and outdoor landscape broadleaf plants, grasses, and palms produced by traditional floricultural and nursery techniques within greenhouses, shaded structures, and other environments significantly modified to favor healthy, rapid, and profitable plant growth.

Ornamentals include annual, biennial, or perennial plants. They may be field grown in native or **amended soils** and then harvested and marketed

amended soils soils to which fertilizers or other growth aids have been added

A number of rhododendron species and hybrids grow in the maritime climate at Broughton-in-Furness, Cumbria, England.

with native soils intact. This form of horticulture is generally referred to as "balled and burlapped" (B&B) plant production even though burlap may not be used in their harvest. They may also be harvested without soil and referred to as "bare root." The most popular method of growing ornamental plants is in soilless growing media within containers. Soilless growing media are most often natural organic materials such as peat or tree bark mixed with a mineral component such as sand or perlite.

Ornamental plants comprise one of the economically and environmentally most important segments of American horticulture. U.S. Department of Agriculture farm income estimates from the production of greenhouse and nursery crops were $11 billion in 1997. California, Florida, Texas, and North Carolina were the top states producing ornamental plants. SEE ALSO Horticulture; Horticulturist; Landscape Architect; Orchidaceae; Propagation.

Richard E. Bir

Palms

vascular related to transport of nutrients

The palm family, Arecaceae, is primarily a tropical family of tree, shrub, and vining monocotyledonous plants, remarkable for the size that many attain without secondary growth (the ability to regenerate **vascular** tissue in their stems as is present in woody dicots). There are at least twenty-seven hundred species of palms, arranged in about two hundred genera. Palms have the largest leaves of any plant, and their leaves are either fan-shaped (palmate, like a hand) or featherlike (pinnate, with many individual leaflets arranged along a central axis). The stems may be solitary or clustering. In time, many palms form tall woody trunks with the leaves clustered in an aerial crown. Palm flowers are individually small, but are contained in often large flower stems (inflorescences) that appear from within the leafy crown or below the sheathing leaf bases. The majority of palms bear male

Coconut palms in Florida.

and female flowers on the same flower stem, but a number of species may produce separate male or female plants; relatively few palms produce bisexual flowers. A handful of palms grow for many years, flower and fruit once, then die. Most palms are pollinated by insects. Palm fruits range from pea-sized to nearly 18 inches wide. The fruit is either fibrous or fleshy, sometimes berrylike. Palms are important components of tropical rain forests worldwide, but many also occur in seasonally dry tropical **ecosystems**, including savannas. A few species are mangrovelike, growing in brackish estuaries near the sea. About twelve species are native to the southern United States, the majority in Florida. Coconut, African oil palm, and date palm are the three most important crop species, but many others are significant sources of food, fiber, wax, and construction material in tropical nations. SEE ALSO MONOCOTS; TREES.

ecosystem an ecological community together with its environment

Alan W. Meerow

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Palynology

Palynology is the study of plant pollen, spores, and certain microscopic planktonic organisms (collectively termed palynomorphs) in both living and fossil form. Botanists use living pollen and spores (actuopalynology) in the study of plant relationships and evolution, while geologists may use fossil pollen and spores (paleopalynology) to study past environments, **stratigraphy,** historical geology, and paleontology.

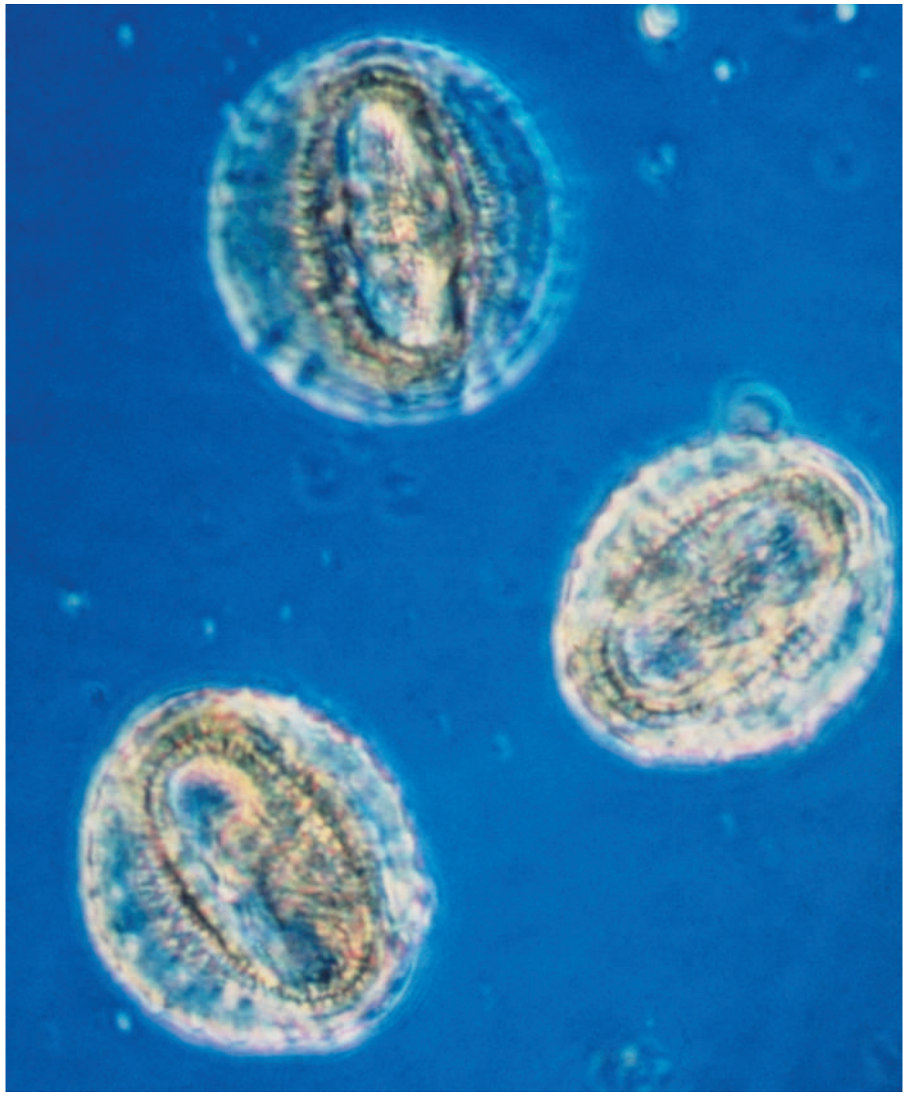
stratigraphy the analysis of strata (layered rock)

The oil industry is credited with demonstrating the usefulness of palynomorphs in the study of stratigraphic sequences of rocks and the potential for oil and gas exploration. Because palynomorphs are resistant to decomposition and are produced in great abundance, their recovery from rocks and sediments via special and careful chemical treatments is possible and provides scientists with information needed to describe plant life of past ages. By describing the sequence of selected palynomorphs through the rock layers of Earth, stratigraphers (scientists who study the rock layers of Earth) are able to correlate rocks of the same age and may therefore locate and correlate layers that contain oil or natural gas.

Palynomorphs found in the gut of early humans, and those found with **artifacts** found at their grave sites have been used to understand the diets and hunting or farming practices of these early people. For instance, the pollen and spores found in the feces of humans living seven thousand years ago allowed scientists to describe the changes in the diets through several generations of native people in northern Chile.

artifacts pots, tools, or other cultural objects

Melissopalynology is the study of pollen in honey, with the purpose of identifying the source plants used by bees in the production of honey. This is important to honey producers because honey produced by pollen and nectar from certain plants as mesquite, buckwheat, or citrus trees demand a higher price on the market than that produced by other plant sources. Some plants



Micrograph of pollen grains.

may produce nectar and pollen that is harmful to human health. A careful examination of the pollen types found in honey may identify these toxic plants, and the honey produced may be kept out of the commercial market.

Palynology is a useful tool in many applications, including a survey of atmospheric pollen and spore production and dispersal (aerobiology), in the study of human allergies, the archaeological excavation of shipwrecks, and detailed analysis of animal diets. Entomopalynology is the study of pollen found on the body or in the gut of insects. It is useful for determining insect feeding and migratory habits, especially as it involves economically important insects (e.g., the boll weevil). Forensic palynology, or the use of pollen analysis in the solving of crimes, is used by law enforcement agencies around the world. SEE ALSO DENDROCHRONOLOGY; FORENSIC BOTANY; POLLINATION BIOLOGY.

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Paper

Paper is a flexible web or mat of pulp fibers of plant (usually wood) origin. It is widely used for printing, packaging, and sanitary applications and also has a wide variety of specialized uses. Paper is formed from a dilute aqueous slurry of pulp fibers, fillers, and additives. Fillers are **inert** materials such as calcium carbonate, clay, and titanium dioxide that make printing papers whiter and increase opacity (the ability to read print on one side of the paper without print on the other side of the paper showing through). Additives are materials used to improve the papermaking process and modify the final product. Additives include dyes, strength agents, and sizing agents (used to make paper resistant to water penetration).

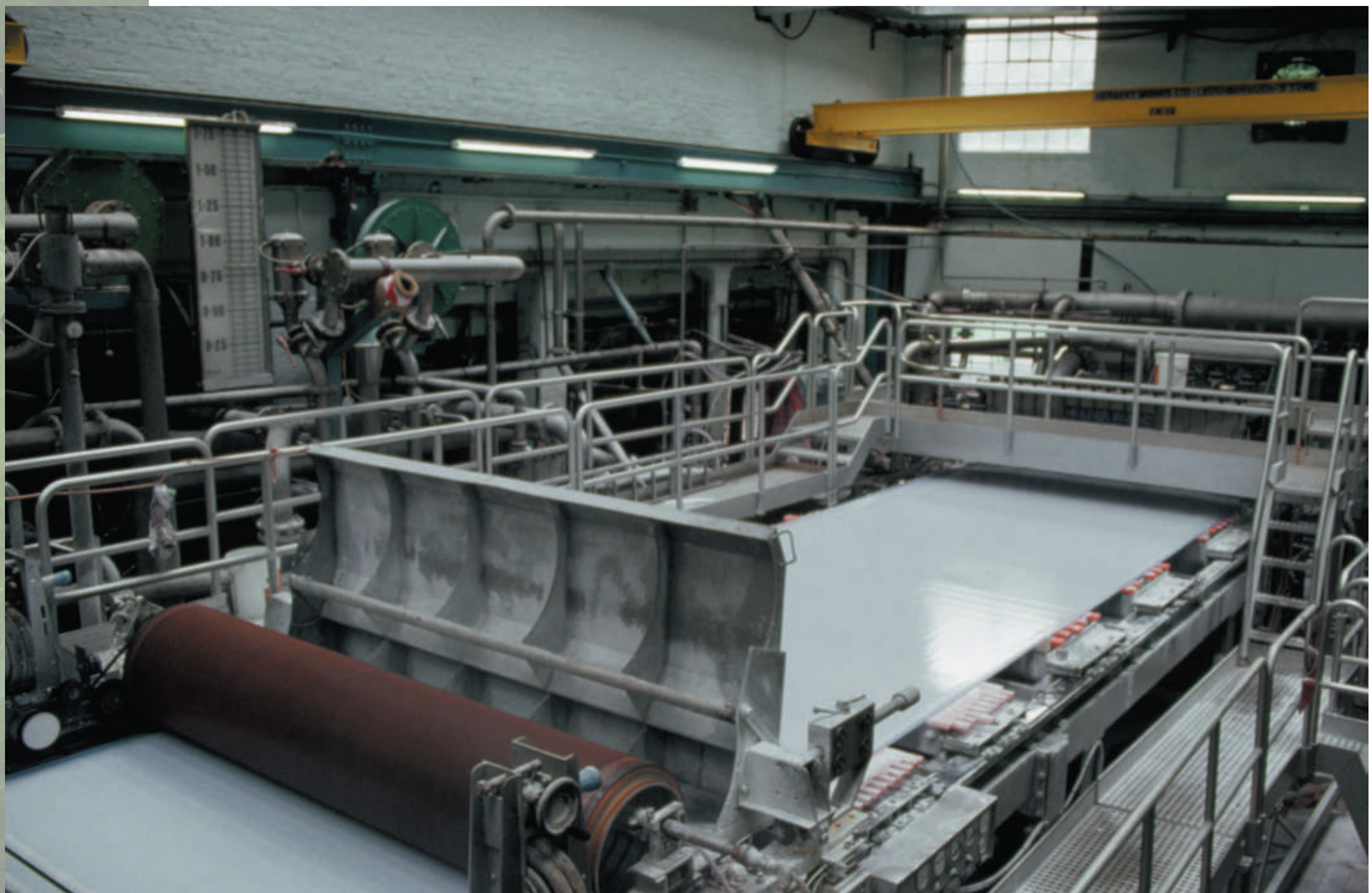
inert incapable of reaction

Pulp is obtained by mechanical or chemical means or by a combination of the two. The two most common pulping methods are thermomechanical pulping and kraft chemical pulping. Thermomechanical pulp accounts for about 20 percent of pulp production in North America. The process consists of introducing wood chips between two large metal discs (on the order of 2 meters in diameter) that have raised bars on their surfaces and that rotate in opposite directions. The discs are in a pressurized refiner that operates at a temperature of 130°C. The combination of mechanical action and steam forms a wood pulp. This wood pulp retains the original lignin of the wood so the paper made from it is not very strong and yellows with age. Mechanical pulp is the chief component of newsprint.

Kraft pulp is formed by cooking wood chips in a highly alkaline aqueous solution at 170°C. It accounts for about 70 percent of pulp production in North America. In this process most of the lignin is removed. The brown pulp is used in sack paper and for the production of corrugated boxes. The bleached pulp is used in white printing papers and tissue papers.

Wood fiber accounts for about 98 percent of pulp production in North America, while globally it accounts for about 92 percent of pulp production. About two-thirds of the wood comes from softwoods because their high fiber length (3 to 5 millimeters) produces strong paper. The short fibers of hardwood species (approximately 1 millimeter) are used with softwood fibers in printing papers to achieve high strength and surface smoothness. Major nonwood sources of fiber, in decreasing levels of global production, include straw (especially wheat), sugarcane residue, bamboo, reeds, and cotton linters. Hemp fibers can also be used, but their fibers are so long that they must be cut in order to make paper from them.

The paper machine continuously forms, drains water, presses, and dries the web of paper fibers, using a single continuously moving plastic screen. The pulp slurry that is applied to the wire consists of 3 to 6 kilograms of dry fiber per 1,000 kilograms of water. Water is then removed by gravity, vacuum, pressing rolls, and, finally, heat in the drier section of the machine.



At a paper mill, wet pulp is spread onto a moving belt from where the water is drained away.

Twin wire machines form the web between two plastic screens, and cylinder machines form several layers of paper that are combined to form heavyweight boards. Paper is converted to a wide variety of products in operations that may include trimming, rewinding onto smaller rolls, cutting into sheets, coating, printing, and box making. SEE ALSO Economic Importance of Plants; Fiber and Fiber Products; Forestry; Trees; Wood Products.

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Parasitic Plants

morphology shape and form

The parasitic mode of existence is frequently encountered among all life forms, including flowering plants. In this discussion a plant will be considered parasitic only if it produces a haustorium, the modified root that forms the **morphological** and physiological link to another plant (the host). Some plants, such as the ghostly white Indian Pipe (*Monotropa*) are often called parasites, but are more properly termed mycotrophs (Greek *mykes*, meaning "fungus," and *trophos*, meaning "feeder"). Mycotrophs, which occur in many plant families, lack chlorophyll and are nonphotosynthetic, and their

PARASITIC PLANT FAMILIES

Family	Common Name	Number of Genera (approximate)	Number of Species (approximate)	Parasitism Type	Genera Example
Balanophoraceae*	Balanophora family	18	45	Root, holoparasite	*Balanophora, Corynaea, Cynomorium, Thonningia*
Cuscutaceae†	Dodder family	1	160	Stem, hemiparasite and holoparasite	*Cuscuta*
Hydnoraceae	Hydnora family	2	15	Root, holoparasite	*Hydnora, Prosopanche*
Krameriaceae	Krameria family	1	17	Root, hemiparasite	*Krameria*
Lauraceae	Laurel family	1	20	Stem, hemiparasite	*Cassytha*
Lennoaceae	Lennoa family	2	5	Root, holoparasite	*Lennoa, Pholisma*
Santalales	Sandalwood order				
Loranthaceae	Showy mistletoe family	74	700	Stem and root, hemiparasite	*Amyema, Phthirusa, Psittacanthus, Tapinanthus*
Misodendraceae	Feathery mistletoe family	1	8	Stem, hemiparasite	*Misodendrum*
Olacaceae	Olax family	29	193	Root, hemiparasite	*Schoepfia, Ximenia*
Opiliaceae	Opilia family	10	32	Root, hemiparasite	*Agonandra, Opilia*
Santalaceae‡	Sandalwood family	40	490	Root, hemiparasite	*Comandra, Santalum, Thesium*
Viscaceae	Christmas mistletoe family	7	350	Stem, hemiparasite	*Arceuthobium, Phoradendron, Viscum*
Rafflesiaceae§	Rafflesia family	8	50	Stem and root, holoparasite	*Cytinus, Rafflesia*
Scrophulariaceae‖	Figwort family	78	1940	Root, hemiparasite and holoparasite	*Agalinis, Buchnera, Castilleja, Epifagus, Euphrasia, Pedicularis, Orobanche, Rhinanthus, Striga*

* Including Cynomoriaceae.
† Sometimes placed in Convolvulaceae (morning glory family).
‡ Including Eremolepidaceae.
§ Including Apodanthaceae, Cytinaceae, and Mitrastemonaceae.
‖ Including Orobanchaceae.

roots are associated with mycorrhizal fungi, which surround tree roots. Bromeliads such as Spanish moss (*Tillandsia*) and some orchids are also sometimes mistaken for parasites, but these plants are actually epiphytes (Greek *epi*, meaning "upon," and *phyton*, meaning "plant"). Epiphytes use the other plant simply as a support and do not derive water or nutrients directly from their tissues. In true parasitic plants, the haustorium physically penetrates the host stem or root thus connecting to the water-conducting and/or sugar-conducting tissues (xylem and phloem, respectively).

The degree of nutritional dependence on the host varies widely among parasitic plants. Some parasites are photosynthetic and can therefore produce their own food from sunlight as is done by other green plants. Such hemiparasites include root parasites such as Indian paintbrush (*Castilleja*, Scrophulariaceae) and stem parasites such as mistletoes (Loranthaceae, Viscaceae; see accompanying table). Some root hemiparasites can actually grow to maturity in the absence of a host plant, and hence are termed **facultative** hemiparasites. Others, such as the mistletoes, must attach to a host in order to complete their life cycle and are thus referred to as **obligate** hemiparasites. Hemiparasites can be considered xylem parasites in that they derive only water and dissolved minerals from their hosts. In contrast, holoparasites, being nonphotosynthetic, must also obtain the carbohydrates found in host phloem.

facultative capable of but not obligated to

obligate required, without another option

Parasitism has evolved in **angiosperms** at least nine independent times, but, interestingly, not in monocots (grasses, palms, lilies, etc.). There exists more than 270 genera and 4,000 species of parasitic plants worldwide. Holoparasitism has evolved at least six times independently. In two families

angiosperm a flowering plant

Dodder tendrils choking a pickleweed plant.

chloroplast the photosynthetic organelle of plants and algae

genome the genetic material of an organism

pathogen disease-causing organism

mycelium the vegetative body of a fungus, made up of threadlike hyphae

(Cuscutaceae and Scrophulariaceae) both hemi- and holoparasites can be found. Members of these families represent important organisms for studying the genetic changes that occur when photosynthesis is lost. For example, a root parasite of beech trees (*Fagus*) found in Eastern North America is called beechdrops (*Epifagus*). The complete deoxyribonucleic acid (DNA) sequence of the beechdrops **chloroplast genome** has been obtained and is less than half the size of a typical photosynthetic plant, mainly owing to the loss of genes specifically involved in photosynthesis.

Other members of Scrophulariaceae represent some of the most economically damaging **pathogens** of crop plants in Africa, the Middle East, and Asia. Witchweed (*Striga*) is a devastating pest on maize (corn), sorghum, and other grasses, while broomrape (*Orobanche*) parasitizes sunflowers, tomatoes, and beans. Similarly, the spaghetti-like dodder (*Cuscuta*) can become a problem weed on crops such as alfalfa. These parasites are difficult to eradicate because they produce thousands of tiny, dustlike seeds that persist in the soil and are easily moved from site to site. In North America, the genus *Arceuthobium* (dwarf mistletoe) destroys commercially important trees in the pine family (Douglas-fir, hemlock, pine, etc.). Unlike other members of its family (Viscaceae) whose seeds are bird-dispersed, dwarf mistletoes have evolved a fruit that explosively expels the sticky seed, which can reach a velocity of 27 meters per second and can travel up to 16 meters.

Although some parasitic plants are weeds, the vast majority are benign and often go unnoticed by the casual observer. Some of the most spectacularly beautiful flowers that exist in nature can be found in the showy mistletoe family (Loranthaceae). Many species produce long, tubular red flowers that are bird-pollinated. Indeed, the mistletoe bird (*Dicaeum*) effects pollination when feeding upon the nectar and aids in seed dispersal when feeding on the fruits, a good example of coevolution.

Certainly, no treatment of parasitic plants would be complete without mention of *Rafflesia*, the queen of the parasites. This holoparasite has no stems, leaves, or roots but exists within the host vine (*Tetrastigma*, Vitaceae) as a fungal-like **mycelium** until flowering. At that time, the flower emerges from the host as a small, golf-ball sized bud and continues to grow until it is the size of a cabbage. Eventually it opens as a flower that may exceed 1 meter in diameter—the largest flower in the world. The spotted red flower has five leathery petals surrounding a deep cup that exudes a stench like that of rotting flesh, thus attracting flies (the pollinators). All species of *Rafflesia* are endangered owing to habitat loss in Malaysia, Indonesia, and the Philippines. SEE ALSO Endangered Species; Epiphytes; Fungi; Interactions, Plant-Plant; Mycorrhizae; Record-Holding Plants.

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Pathogens

A pathogen is an agent that causes disease. The agent usually is a microorganism, such as a fungus, bacterium, or virus. The most numerous and prominent pathogens of plants are the fungi, but many plant diseases are also caused by bacteria and viruses. Although the diseases caused by phytoplasmas are similar to those caused by viruses, these pathogens are actually a kind of bacterium. A few diseases are caused by viroids, agents that are similar to but are even simpler than viruses. Other pathogens include nematodes (roundworms), which attack many types of plants, and 2,500 species of **angiosperms** that live parasitically on other plants. Relatively few of the angiosperms are economically important pathogens.

angiosperm a flowering plant

A pathogen usually initiates disease by parasitizing a host, that is, taking its organic nutrients. However, in a few cases the host actually benefits by the presence of the parasite. Mycorrhizal fungi attack roots and live parasitically in the roots. But infected roots are much more effective than nonmycorrhizal roots in obtaining mineral nutrients, especially phosphorus. Where the level of phosphorus in the soil is low, the plants with mycorrhizal roots are much healthier. Since the parasite actually benefits the plant, it does not cause disease and is not considered a pathogen.

Types of Pathogens

Fungi. Like all **eukaryotic** organisms, fungal cells have nuclei, a well-defined **endoplasmic reticulum** with ribosomes, and cell **organelles** such as mitochondria. The fungal body consists of **filamentous** strands called **hyphae** that collectively make up a mycelium. Sometimes the hyphae become compressed, forming a tissue such as that found in a mushroom fruiting body.

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

endoplasmic reticulum membrane network inside a cell

organelle a membrane-bound structure within a cell

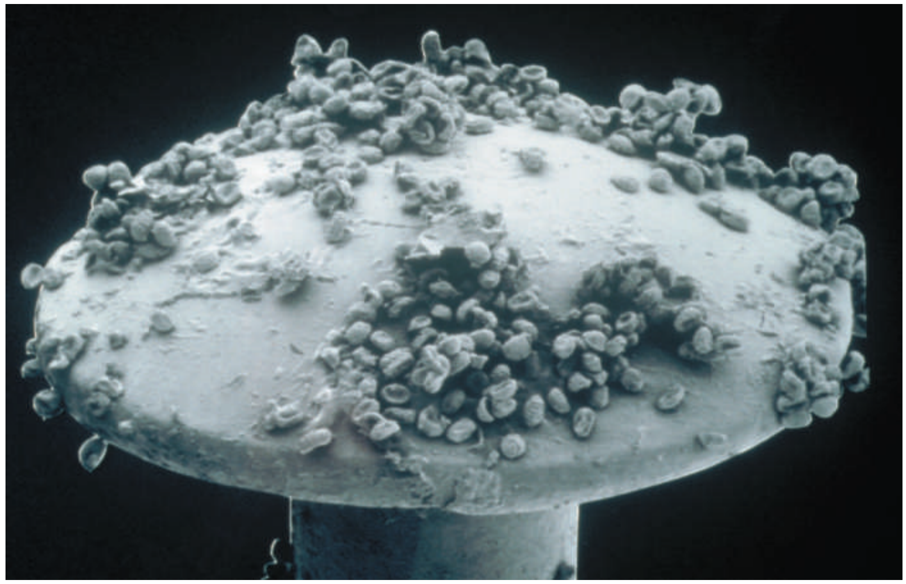
filamentous thin and long

hyphae the threadlike body mass of a fungus

Fungi are classified in the kingdom Fungi, separate from all other organisms. There are many different groups within the kingdom, and most groups have prominent plant pathogens. Of particular note are the Ascomycetes, Fungi Imperfecti, and some of the Basidiomycetes. Ascomycetes produce sexual spores called ascospores that are vital in survival between hosts. They also produce asexual spores called conidia that play a major role in the spread of disease during the growing season. The Fungi Imperfecti usually are ascomycetes that have lost the ascospore (sexual) stage. Sometimes they produce ascospores but have been classified according to the conidial stage because of its importance in the disease cycle. It is valid to classify a fungus based either on its perfect (sexual) state or on its imperfect (asexual) state.

The Basidiomycetes are extremely common in nature, but only the rusts and smuts are notable plant pathogens. While most basidiomycetes produce basidiospores in a fruiting body such as a mushroom, in rusts and smuts the basidiospores are produced from a specialized, overwintering spore called a teliospore. The rust fungi are especially common and usually have a complex sexual cycle with four spore stages and two different hosts required for completion of the sexual cycle. Rusts also produce an asexual spore called a uredospore that is responsible for spread of disease during the growing season.

A fourth group of fungi, the Oomycetes, has long been recognized to be very different from other fungi in both morphology and chemistry. They



Roundworm eggs on a pin head. These pathogenic nematodes are usually found in soil and use their stylet mouthpart to penetrate and feed on roots.

motile capable of movement

produce overwintering sexual spores called oospores and asexual **motile** spores (zoospores) that spread disease during the season. The current trend is to place these fungi in a kingdom other than Fungi. The Oomycetes contain the *Pythium* and *Phytophthora* species and the downy mildews, plant pathogens that are of worldwide importance. Regardless of classification, these pathogens will continue to be treated much the same as true fungi by those who work with plant diseases.

The potato late blight disease caused by *Phytophthora infestans* that resulted in famine in Ireland in 1845 and 1846 first brought the attention of the world to plant diseases. At that time many thought that fungi arose spontaneously in diseased plants and did not themselves cause disease. However, publications by the German scientist Anton de Bary beginning in 1853 convincingly demonstrated the prominent role fungi play as plant pathogens.

Bacteria. The plant pathogenic bacteria are rod-shaped eubacteria. They are prokaryotes, having a chromosome but no nucleus. The cytoplasm has ribosomes but no endoplasmic reticulum and no organelles. The cells have a cell wall and may or may not have **flagella**.

flagella threadlike extension of the cell membrane, used for movement

The first bacterium shown to cause a plant disease, fire blight of pome fruits, was reported by Thomas Burrill in Illinois in 1878. However, it was the research by Erwin F. Smith from 1890 to 1915 that demonstrated the importance of these agents as plant pathogens.

macromolecules a large molecule such as a protein, fat, nucleic acid, or carbohydrate

Viruses. Viruses are nucleoprotein **macromolecules**. They contain genetic information, either ribonucleic acid (RNA) or deoxyribonucleic acid (DNA), which is covered by protein subunits. Plant pathogenic viruses usually contain RNA rather than DNA. Since viruses are not cellular organisms, they express lifelike characteristics only when within a susceptible host cell. Additionally, since they are not cellular, they do not obtain organic nutrients directly from the host. Instead, the RNA or DNA of the virus directs the metabolic machinery of the host cell to use organic nutrients present in the cell. Various chemical reactions lead to symptom expression as well as production of new virus particles.

DISTINGUISHING CHARACTERISTICS OF VARIOUS PATHOGENS

Character	Fungi	Bacteria	Viruses	Phytoplasmas	Nematodes
Body type	Hyphae make up a mycelium (eukaryotic)	Cells with cell walls (prokaryotic)	Nucleoprotein (not cellular)	Cells with no cell walls (prokaryotic)	Worms with organ systems, males and females
Inoculum	Overwinter by ascospores, teliospores, and oospores; spread of disease by conidia, zoospores, uredospores	Cells	Virus particles	Cells	Larvae
Dissemination	Wind and splashing rain	Splashing rain	Transmission by insects, mechanically, or planting stock	Transmission by insects	Soil movement, running soil water
Penetration	Direct by appressorium and penetration peg; some through wounds or natural openings	Through natural openings (stomata) or wounds	Through wounds (insects) or planting stock	Through wounds (insects)	Direct with stylet mouthpart
Host-parasite relation	Inter- and intracellular; intercellular with haustoria	Intercellular	Intracellular in parenchyma or phloem tissue	Intracellular in phloem tissue	Intercellular with stylet inserted in host cells

Tobacco mosaic disease was shown in the 1890s to be caused by a submicroscopic infectious agent later determined to be a virus, now called tobacco mosaic virus.

Viroids. A viroid is a small, infectious piece of RNA. Unlike a virus, it has no protein, but it behaves as a plant parasite much the same as a virus. In 1967, Theodor Diener and William Raymer reported on the basic characteristics of the agent causing spindle tuber of potato, and in 1971 Diener named these agents "viroids." About twenty diseases have been shown to be caused by this type of pathogen.

Phytoplasmas. Phytoplasmas are prokaryotic cellular organisms. They represent a separate group of bacteria, having no cell wall or flagella. Much like viruses, they are transmitted by insects and cause phloem necrosis-type diseases. These diseases, having yellows witches'-broom-type symptoms, were thought to be caused by viruses until 1967 when Yoji Doi and others in Japan showed that the disease-inducing agents are mycoplasma-like organisms. Some of these pathogens, especially the aster yellows phytoplasma, have a wide host range and attack plants in many families.

For many years these plant pathogens were identified as mycoplasma-like organisms, but they now are called phytoplasmas. Although viruses and phytoplasmas are very different biological agents, similarities in transmission and in host-parasite interactions and symptoms make it easy to understand why researchers before 1967 thought all these diseases were caused by viruses.

Nematodes. Plant pathogenic nematodes (roundworms) are usually found in soil. These plant pathogens have a stylet (spearlike) mouthpart that is used to penetrate and feed on roots. Although root knot nematode diseases have been well known since the 1850s, it was not until the period between

1920 and 1940 that research by many investigators showed the full significance of these agents as plant pathogens.

Angiosperms. Like typical flowering plants, parasitic angiosperms have stems, leaves, flowers, and seeds. They do not have true roots but produce a structure that penetrates stems and unites with the **vascular** system of the host. The leaves may or may not have **chloroplasts**, but these pathogens are completely dependent on the host for water and mineral nutrients. Dwarf mistletoe is a prominent pathogen of coniferous forest trees, and the dodders attack many crops worldwide. Leafy mistletoe, known as a popular household Christmas decoration, attacks hardwood trees but is seldom a leading pathogen.

vascular related to transport of nutrients

chloroplast the photosynthetic organelle of plants and algae

Insects. Insects do not merely feed on plants; they often produce **toxins** and growth substances that cause diseaselike symptoms. Some of the biological interactions are similar to those that occur with nematodes. However, there are hundreds of thousands, perhaps millions, of insect species, and their life cycles and behavior may be very complex. Although the phenomenon may be much the same, insect problems are worked on by experts (entomologists), and the insects usually are not thought of as pathogens. They are, however, major **vectors** of diseases, including those caused by viruses and phytoplasmas and some fungi and bacteria.

toxin a poisonous substance

vector carrier of disease

How Pathogens Cause Disease

Pathogens **impede** normal growth of plants in many ways. They attack and kill seeds and seedlings (damping off diseases). They invade and kill roots, preventing absorption of water and mineral nutrients (root rots). They invade and plug xylem tissue, preventing movement of water and minerals to leaves and growing points (vascular wilts). They kill leaves, preventing photosynthesis and production of carbohydrates (leaf spots and blights, downy mildews, powdery mildews, and rusts). The phloem tissue may be invaded and killed, preventing translocation of the carbohydrate produced in photosynthesis to other parts of the plant (phloem necrosis). After the crop has been produced, pathogens may rot fruits and vegetables in transit or storage or in the marketplace (fruit and vegetable rots). A few pathogens cause disease by inducing abnormal growth, thus stunting normal growth (galls).

impede slow down or inhibit

Damping Off. Many fungi that live in the soil invade and kill seeds or seedlings. This is called damping off. Beyond the seedling stage, a plant is no longer susceptible to damping off. There is no resistance but seed treatments with fungicides usually provide effective control.

Root Rots. Roots may be rotted by many fungi living in the soil. The resulting lack of water and mineral nutrients stunts growth and causes a general yellowing due to lack of chlorophyll. There usually is little resistance, and chemical controls are ineffective. **Crop rotation** may hold crop losses to acceptable levels.

crop rotation alternating crops from year to year in a particular field

Vascular Wilts. Vascular wilts, diseases of the xylem tissue, are caused by fungi and bacteria. Fungi causing this disease are soilborne. They infect roots and grow through the plant, colonizing the xylem. Bacteria that cause vascular wilts are transmitted by insects or penetrate leaves through **stomatal** openings. They invade xylem tissue through pits in the xylem vessel

stomata openings between guard cells on the underside of leaves that allow gas exchange

Cedar-apple rust gall on a cedar tree

cell walls and become **systemic** in the plant. Vascular wilts caused by both fungi and bacteria reduce movement of water and mineral nutrients to stems and leaves, resulting in symptoms of wilting and yellowing. There is no chemical control but genetic resistance may be helpful. Crop rotation is important in combating vascular wilts.

systemic spread throughout the plant

Leaf Diseases. Many fungi and bacteria attack leaves, causing leaf spots and blights. The downy and powdery mildews also cover the leaves with fungal structures further reducing photosynthesis. Both of the mildews and the rusts eventually kill leaf tissue, but since all three are **obligate parasites,** they no longer can obtain nutrients after the leaves are dead. Resistance to these fungal diseases often is available, and chemical controls usually are effective. Most of the fungicides applied to crops are used to control leaf diseases. There are fewer leaf diseases caused by bacteria, and this is fortunate because genetic resistance is seldom available and chemical controls are usually ineffective.

obligate parasite without a free-living stage in the life cycle

Phloem Necrosis. Viruses and phytoplasmas are transmitted by insect vectors that feed on leaves. The vectors often feed on the phloem tissue, directly depositing the pathogen in the tissue. These agents then become systemic in the phloem tissue, killing the phloem cells (necrosis) and preventing translocation of organic nutrients throughout the plant. Typical symptoms are stunting, yellowing, mosaic (different shades of green and yellow), and mottling (blotches of different colors). There is no chemical control and often little resistance. Cultural practices such as use of healthy planting stock often limit disease incidence.

Fruit and Vegetable Rots. Postharvest rots by fungi and bacteria often cause serious losses. Chemical treatments help control these diseases, but more significant prevention tactics include sanitation and use of proper storage conditions, particularly reduced temperature and increased air circulation.

Galls. Abnormal growth is an extremely common phenomenon and can be caused by many biological agents. The most notable abnormal growth diseases of crops are crown gall, caused by the bacterium *Agrobacterium*, club root of crucifers caused by the fungus *Plasmodiophora brassicae*, and root knot caused by the nematode *Meloidogyne*. Abnormal growth results from action of the same kinds of growth substances that are responsible for normal growth: **auxins**, cytokinins, and gibberellins.

auxin a plant hormone

Recognition and Penetration

Relatively little is known of the biochemistry of recognition of a susceptible host by a pathogen. Fungal and bacterial inoculum (infectious material) is spread at random to both hosts and nonhosts. **Mucilagenous** substances on the surface of the inoculum facilitates adherence to host surfaces. Some host chemicals that serve as signals leading to penetration are known, and some pathogen chemicals that serve as elicitors in disease development have been identified. In some cases penetration occurs but growth in the host is limited, and disease does not develop. Either the agent does not produce the elicitors that lead to infection, or the host produces chemicals that prevent infection. Since viruses and phytoplasmas are brought to hosts by insect vectors, disease may result from an adaptive sequence in which the vector feeds preferentially on the hosts that are susceptible to the pathogen.

mucilagenous sticky or gummy

Fungi usually penetrate leaves by production of a specialized structure called an appressorium. As a fungal hypha grows over the surface of a leaf, the hyphal tip mounds up and becomes cemented to the leaf, forming an appressorium. A specialized hypha, called a penetration peg, grows from the appressorium and penetrates the leaf, largely by mechanical pressure. The penetration peg also may produce cutinase and cellulose **enzymes** that soften the tissue. The leaf **epidermis** is covered by a **cuticle** made primarily of a waxy substance called cutin, and the epidermal cell walls have a high cellulose content. Sometimes a fungus penetrates through a stoma, a hole in the lower epidermis of the leaf formed by two guard cells. Even when a fungus penetrates through a stoma, an appressorium is usually produced. Of course, the penetration peg meets no resistance.

enzyme a protein that controls a reaction in a cell

epidermis outer layer of cells

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

Inside the leaf, fungal hyphae grow between cells (intercellular) and through cells (intracellular) to obtain nutrients. When the leaf dies, the fungus is able to obtain nutrients from the dead cells. The fungi that are obligate parasites (downy mildews, powdery mildews, and rusts) grow intercellularly and produce haustoria (specialized hyphal structures) that penetrate the host cells. The haustoria produce enzymes and obtain nutrients from the host cells. Eventually the cells die, and these fungi are no longer able to obtain nutrients.

Bacteria that attack leaves are disseminated in splashing rain and penetrate through stomata or wounds. The bacteria are found between cells in the host and never penetrate the living cells. Nutrients leaking from the host cells provide sufficient food for the bacteria. After the death of leaves, the bacteria continue to obtain nutrients from the dead cells.

Viruses and phytoplasmas are usually transmitted by insects. Feeding by the insects deposits these agents into the phloem or **parenchyma** tissues. Some viruses can be transmitted by workers in the field. Handling plants causes small wounds and transmits small amounts of contaminated sap. Many viruses attack crops that are **propagated** vegetatively (by bulbs, corms, bud-

parenchyma one of three plant cell types

propagate to create more of through sexual or asexual reproduction

ding, etc.), and the diseases are transmitted through use of infected planting stock. Both viruses and phytoplasmas are obligate parasites and cannot obtain nutrients from tissues that have died.

Nematodes penetrate roots mechanically by use of the stylet mouth part. Once inside they insert the stylet into parenchyma cells of the cortex and obtain nutrients. Some nematodes have a long stylet and feed on plant roots while the body is outside the root. Plant pathogenic nematodes are all obligate parasites, capable of obtaining nutrients only from living host cells.

Role of Enzymes, Toxins, and Phytoalexins

Because cutin and cellulose provide tough, protective barriers for the plant, cutinase and cellulase enzymes are necessary to the penetration of plant hosts by pathogenic fungi. They break down the cutin in the cuticle and the cellulose in the primary cell wall. Hydrolytic (digestive) enzymes also play important roles in pathogenesis. The organic food in the host is usually in the form of complex carbohydrates, fats, and proteins. To be absorbed by pathogens, they must be broken down to their simpler units: simple sugars, fatty acids, glycerol, and amino acids. Common digestive enzymes—amylases, cellulases, lipases, and proteases—produced by pathogens break down these complex foods.

The middle lamella, the area between cells in parenchyma tissue, has a high pectin content. For many diseases pathogenesis involves production of pectolytic enzymes that break down pectin. This causes dissolution and eventually death of the cells. Damping off, root rots, vascular wilts, and fruit and vegetable rots are caused by pathogens that produce large amounts of pectolytic enzymes.

Several toxins have been shown to be produced by plant pathogenic fungi and bacteria. Most of them are nonhost-specific toxins. They usually kill cells but may act on the **permeability** of the cytoplasmic membrane. Although they are involved in pathogenesis, in some cases strains of the pathogen that are unable to produce the toxin still can cause disease. In a few cases the toxin is host-specific and only affects that host at normal toxin concentrations.

permeability the property of being permeable, or open to the passage of other substances

Most plants are resistant to infection because of the presence of preexisting chemicals. However, there are many cases where chemicals that ward off infection are produced by the host only after the pathogen is present. These chemicals are called phytoalexins. This is a rather common phenomenon, with about three hundred chemicals from thirty different families of plants having been identified as phytoalexins. SEE ALSO AGRICULTURE, MODERN; CHESTNUT BLIGHT; DEFENSES, CHEMICAL; DUTCH ELM DISEASE; EUBACTERIA; FUNGI; HERBICIDES; HORMONES; INTERACTION, PLANT-FUNGAL; POTATO BLIGHT.

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Pathologist

Plant pathologists are scientists who work with plant diseases. Trained primarily as biologists, they have expertise both in plant science and microbiology. Whereas in medicine the pathologist is a specialist who analyzes diseased tissues, the plant pathologist is concerned with all aspects of plant disease. All plants are subject to disease, and the work of plant pathologists is central to the management of diseases.

Many plant pathologists may be compared to the general practitioner in medicine, but there are many areas of specialization that may involve the kind of crop or pathogen. Most plant pathologists who work with field crops or vegetables have rather general training in plant pathology, but virologists and nematologists require specialized training because these agents are very different from all other pathogens. Forest pathologists also need unique training, both because the forest is a very different crop and because the common pathogens are different from those that attack agricultural crops. Some plant pathologists are biochemists or molecular biologists who study diseased plants or pathogens. Epidemiologists study the spread of disease in populations and they must be well grounded in mathematics and statistics.

physiology the biochemical processes carried out by an organism

Most jobs taken by plant pathologists require a doctorate degree, but some directors of diagnostic labs have a master's degree. Plant pathologists must be well versed in plant **physiology** and genetics and must have knowl-

A U.S. Department of Agriculture scientist uses tweezers and magnifying goggles to examine citrus roots for fungus.

edge of all disease-causing agents. The study of the fungi is particularly important since these are the most numerous and troublesome pathogens of plants. Courses in plant pathology provide background in disease initiation and progress for each kind of pathogen. This knowledge is used when designing programs for management of disease.

Plant pathologists are employed by universities, federal and state governments, and a wide range of industries. All **land-grant universities** have plant pathologists who are responsible for resident instruction, research, and extension education. Plant pathologists conduct research at state agricultural experiment stations and the U.S. Department of Agriculture, and are employed by federal and state agencies that enforce regulations regarding pesticide use and food safety. Chemical companies employ plant pathologists for production of more effective and safer pesticides, and seed companies use their expertise to produce disease resistant varieties. Many plant pathologists work as consultants or provide service in diagnostic labs.

land-grant university a state university given land by the federal government on the condition that it offer courses in agriculture

The complexity of two interacting living systems—the plant and the pathogen—makes plant pathology a very challenging field. An appealing feature of employment as a plant pathologist is the opportunity for work in a wide range of environments. Teaching may occur on the farm as well as in the classroom, and research may be conducted in the field or greenhouse as well as in the laboratory. Disease **specimens** may be diagnosed in the lab, but disease progress must be evaluated in the field. Plant pathologists have opportunities for research in international centers and for cooperative work with plant pathologists in other countries.

specimen object or organism under consideration

Work by the plant pathologist touches on many important contemporary issues, such as overpopulation, the safety of genetically engineered food, and the effects of pesticides on human health and the environment. But the role played by plant pathologists in the production of abundant, safe food for people of the world is of central importance. SEE ALSO PATHOGENS.

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Peat Bogs

A peat bog is a type of wetland whose soft, spongy ground is composed largely of living and decaying *Sphagnum* moss. Decayed, compacted moss is known as peat, which can be harvested to use for fuel or as a soil additive.

Peat bogs are found throughout the world where cool temperatures and adequate rainfall prevail. Estimates indicate that peatlands (bogs and fens) cover as much as 5 percent of the land surface, primarily in northern temperate and arctic regions. Canada contains approximately 130 million hectares of bogs, while the United States has approximately 7 million hectares.

Bogs are not just any type of wetland, and they require a particular sequence of events in order to form. A bog begins in a low spot where groundwater is close to or above the surface. Such a spot, sometimes called a fen, contains a wide mix of water-tolerant plants, including grasslike plants such

Sphagnum moss grows in a bog near Mount Kosciusko, Australia's highest point. The moss acts as a sponge, and releases the water it has absorbed in winter throughout the rest of the year.

as reeds and sedges, and trees such as alders. Groundwater has a relatively high mineral content, which helps support this variety of plant types. Because water in such low spots is still, oxygen is not replenished quickly, and normal decomposition of dead plants is slowed somewhat by the low oxygen content. When plant deposition exceeds plant decay, the fen begins to fill in, and the uppermost level of the fen loses contact with groundwater. In many wetland areas, this leads to drying out of the wetland and development of a field or woodland. However, if there is sufficient rainfall and other conditions are right, the fen may be transformed into a raised bog—a self-contained wetland that grows up to and even above the surrounding terrain.

ions charged particles

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral; low pH numbers indicate high acidity; high numbers indicate alkalinity

Most plants cannot survive on the low mineral content of rainwater, but the several dozen species of mosses of the genus *Sphagnum* can, and these come to dominate the bog flora. *Sphagnum* removes positive **ions** from the water such as calcium and sodium, leaving positive hydrogen ions, which are acidic. As a result, the **pH** of bog water may be as low as 3.5, about the acidity of tomato juice. As new *Sphagnum* grows atop the partially decayed growth of previous years, it compacts the layers below it into the thick, crumbly, spongelike material known as peat. Other bog plants include the carnivorous sundews (*Drosera* spp.) and acid-tolerant reeds and sedges.

Peat has been harvested as a fuel for millennia, and it is still used this way today. Fuel peat is harvested both commercially and by individuals. Because bog peat is approximately 95 percent water, it must be dried before use. Dried peat is also used as a soil additive in gardens and nurseries, and its harvest and export for this purpose is economically significant to Canada, Sweden, Ireland, and several other countries.

Like other wetlands throughout the world, bogs are threatened by human activities, including draining and filling, and harvesting of peat. Estimates indicate that 90 percent or more of former boglands has been lost in several European countries. SEE ALSO Bryophytes; Carnivorous Plants; Wetlands.

Richard Robinson

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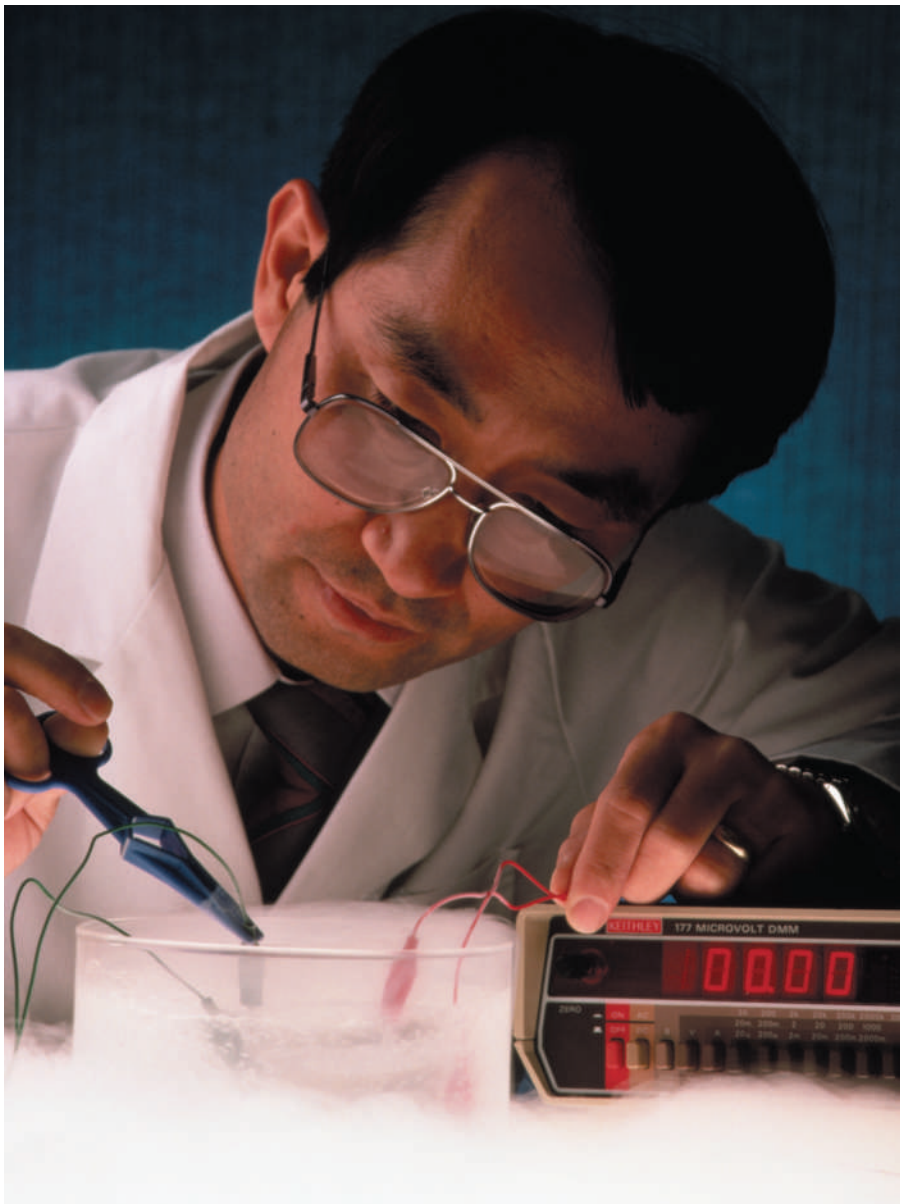
Pharmaceutical Scientist

Pharmacists are professionals whose goals are to achieve positive outcomes from the use of medication to improve patients' quality of life. The practice of pharmacy is a vital part of the complete health care system. Due to society's many changing social and health issues, pharmacists face constant challenges, expanded responsibilities, and increasing growth in opportunities.



A pharmaceutical scientist performing research, holding calipers that grip electrical wires inside a glass container while vapors spread around the container's base.

Pharmacists are specialists in the science and clinical use of medications. They must have the knowledge about the composition of drugs, their chemical and physical properties, and their uses as well as understand the activity of the drug and how it will work in the body. Pharmacy practitioners work in community pharmacies, hospitals, nursing homes, extended care facilities, neighborhood health centers, and health maintenance organizations. A doctor of pharmacy degree (Pharm.D.) requires four years of professional study, following a minimum of two years of pre-pharmacy study.

Pharmacy practitioners may combine their professional activities with the challenge of scientific research. Many pharmacists go on to obtain postgraduate degrees in order to meet the technical demands and scientific duties required in academic pharmacy and the pharmaceutical industry. Students have the opportunity to complete advanced study (graduate work) at pharmacy schools across the United States. Graduate studies may qualify the student for a Master of Science (M.S.) or Doctor of Philosophy (Ph.D.) degree in various areas of pharmaceutical sciences (medicinal and natural products chemistry, **pharmacognosy**, pharmacology, toxicology). These research degrees require an undergraduate bachelor's or a doctor of pharmacy degree. The pharmaceutical scientists are mainly concerned with research that includes sophisticated instrumentation, analytical methods, and animal models that study all aspects of drugs and drug products.

pharmacognosy the study of drugs from natural products

The pharmaceutical industry offers many opportunities to pharmaceutical scientists in research, development, and manufacture of chemicals, prescription and nonprescription drugs, and other health products. Colleges and schools of pharmacy present options in teaching and in academic research. Pharmaceutical scientists may also be employed in a variety of federal and state positions including with the U.S. Public Health Service, the Department of Veterans Affairs, the Food and Drug Administration, the Centers for Disease Control, and in all branches of the armed services. In addition, they may also be engaged in highly specialized jobs such as science reporters, as experts in pharmaceutical law, or as drug enforcement agents, or they may specialize in medicinal plant cultivation and processing.

As society's health care needs have changed and expanded, there has been an increased emphasis on the use of herbal remedies as dietary supplements or the search for new prescription drugs from natural sources such as microbes and plants. As a result, an increased number of pharmaceutical scientists hold doctoral degrees in natural products chemistry, pharmacognosy, or medicinal chemistry and are involved in **biodiversity** prospecting for the discovery of new medicines. At the turn of the twenty-first century there exists a shortage of specialists in this area, and they are in great demand if they are also trained in **ethnobotany.**

biodiversity degree of variety of life

ethnobotany the study of traditional uses of plants within a culture

There are many opportunities and great potential for advancement and competitive salaries within a pharmacy science career. In 1999, starting annual salaries average between $50,000 and $65,000, depending on location. SEE ALSO Ethnobotany; Medicinal Plants; Plant Prospecting.

Barbara N. Timmermann

Photoperiodism

Photoperiodism is an organism's response to the relative lengths of day and night (i.e., the photoperiod). We have always known that plants are tied to the seasons: each kind of plant forms flowers at about the same time each year; for example, some in spring, some in summer, some in autumn. Botanists knew that plants responded in various ways to temperature and other changes in the environment, but it was not until World War I (1914–18) that anyone tested plant responses to photoperiod. At that time Wightman W. Garner and Henry A. Allard at the U.S. Department of Agriculture in Maryland began to control various parts of the environment in their greenhouses to see if they could make a new **hybrid** tobacco bloom in summer rather than only in winter. Nothing worked until they put plants into dark cabinets for various times overnight in midsummer. Long nights caused their tobacco plants to flower, and they soon tested other species. They published their results in 1920.

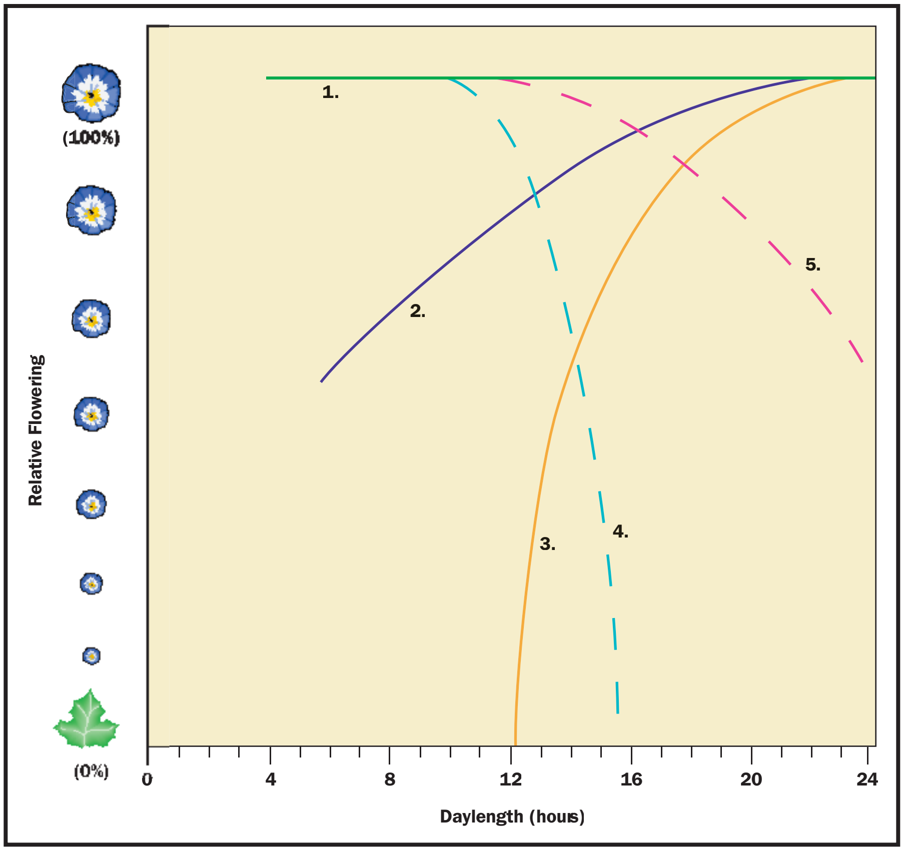
hybrid a mix of two varieties or species

Long-Day, Short-Day, and Day-Neutral Plants

Garner and Allard (and others) discovered that tobacco, soybeans, chrysanthemums, and several other species flowered only when the days were shorter than some maximum length and the nights were longer than some minimum length, with the exact times depending on the species. They called plants with this response "short-day plants." Such plants flower in either spring or fall. Radishes, spinach, a different species than their experimental tobacco, and other species had an opposite response: they flowered only when days were longer than some minimum length and nights were shorter than some maximum length. These are called long-day plants. These plants flower primarily in the summer. Tomato, sunflower, yet another species of tobacco, and several other species formed flowers almost independently of daylength. These are called day-neutral plants.

Later work by other investigators found a very few species, called intermediate-day plants, that flowered only when the days were neither too

Short-day plants, which flower when the days are shorter than some maximum length and the nights were longer than some minimum length, include these Autumn Days chrysanthemums.



A diagram illustrating the principle of flowering responses to different daylengths. Curve 1 shows the response of a truly day-neutral plant that flowers in response to all daylengths. Such plants are rare. Curve 2 shows a day-neutral plant that flowers in response to all daylengths but is promoted in its flowering by longer days. Note that the responses of almost all plants become somewhat complex at the very short daylengths—shorter than 4 to 6 hours. Curve 3 shows a typical absolute long-day plant that requires long days to flower and remains vegetative almost indefinitely on short days. The curve that is shown might represent henbane (*Hyoscyamus niger*); unless days are longer than about 12 hours it remains vegetative. In that case, the 12 hours is the critical daylength. Other species might have other critical daylengths. Curve 4 shows a typical absolute short-day plant that remains vegetative on long days but flowers when the days reach a critical daylength. The curve is drawn to represent cocklebur (*Xanthium strumarium*), which requires at least 8.3 hours of darkness to form flowers (the critical night). Note that both henbane and cocklebur flower when days are between 12 and 15.7 hours long. (Again, other species of short-day plants can have different critical days—or critical nights.) Curve 5 shows a typical day-neutral plant that is promoted in its flowering by shorter days but will eventually flower at any daylength.

short nor too long. The opposite is also known: some plants flower on long or short but not on intermediate days. A few species have an absolute photoperiod requirement while others are promoted by some photoperiod but eventually flower without it. Although light intensity sometimes influences the response, typically plants respond not to the amount of light but only to the durations of light and dark. A short-day cocklebur plant (*Xanthium strumarium*), for example, blooms only when nights are longer than about 8.3 hours, while long-day henbane (*Hyoscyamus niger*) flowers only when the nights are shorter than about 12 hours.

Although the effective durations of light and dark are typically almost independent of temperature, temperature often influences the type of response.

Some species, for example, may require cool temperatures followed by long, warmer days (e.g., sugar beet). Some species may be day-neutral at one temperature and have a photoperiod requirement at another temperature.

Many plant responses in addition to flowering are controlled by photoperiodism. (Animal breeding times, migration times, fur color, and many other phenomena are also influenced by photoperiod.) Photoperiod influences stem lengths, dormancy and leaf fall in autumn, germination of some seeds, tuber and bulb formation, and many other plant manifestations. In flowering, it is the leaf that senses the photoperiod, so some signal must be sent from the leaf to the buds where flowers form. Although numerous attempts have failed to isolate a chemical signal for flower formation—a hormone—most researchers still feel confident that such a so-called **florigen** must exist.

florigen a substance that promotes flowering

Measuring Time

The essence of photoperiodism is the measurement of time, the durations of day and night. Early experiments showed that the night was especially important for many species. Interrupting the night with even a brief period of light (seconds to an hour or two, depending on species and light intensity) stops the short-day response or promotes the long-day response. If the total of light plus dark adds up to more or less than twenty-four hours, it is the dark period that seems to be important. More recent experiments, however, show that photoperiod-sensitive plants measure the durations of both day and night. Time measurement in photoperiodism is clearly related to **circadian** leaf movements and other manifestations of the biological clock.

circadian "about a day"; related to a day

How do the plants *know* when it is light or dark? The pigment phytochrome, so important in many plant responses, couples the light environment to the mysterious biological clock. Phytochrome exists in two forms, both of which absorb certain wavelengths (colors) of light. One form, called P_r, absorbs red light, which converts it to the other form, P_{fr}. P_{fr} absorbs longer wavelengths of light, called far red, which convert it back to P_r. During the day, red light predominates so most of the pigment is in the P_{fr} form, signaling to the clock that it is light; the clock measures how long it is light. As it begins to get dark, the P_{fr} begins to break down, and some of it is spontaneously converted to P_r. This drop in P_{fr} level signals the clock that it is getting dark, and the clock begins to measure the length of the dark period. When the lengths of both day and night are right for the particular species, the next steps in the response to photoperiod are initiated; for example, florigen may begin to be synthesized.

Much study has gone into understanding these phenomena, and recent work has emphasized the role of specific genes in the flowering process.

Photoperiodism and the Distribution of Plants

Photoperiodism influences the distribution of plants on Earth's surface. As expected, species that require long days for flowering (in spring or summer) occur far from the equator. Short-day species occur in the same regions but flower in late summer. Tropical short-day species also occur, growing only 5° to 20° from the equator. These species detect very small changes in daylength (e.g., one minute per day in March and September at 20° north or south of the equator).

With respect to photoperiod, there can be many ecotypes within a species. For example, the northern ecotypes of short-day cocklebur or lambsquarters (*Chenopodium rubrum*) or the long-day alpine sorrel (*Oxyria digyna*) require longer days and shorter nights to flower than their more southern counterparts. In these examples, the different photoperiod ecotypes within a species are virtually identical in appearance but have different clock settings.

Advantages of Photoperiodism to a Species

The ecotype differences are often clearly of advantage to the species. For example, frost comes much earlier in the year in more northern climates, and the various ecotypes of cocklebur all flower about six to eight weeks before the first killing frost in autumn, allowing time for seed ripening.

Because of photoperiodism, flowering and other responses within an ecotype population of plants are synchronized in time. This is certainly an advantage if the plants require cross pollination; it is essential that all bloom at the same time. Garner and Allard noticed that soybean plants, despite being planted at various times from early spring to early summer, all came into bloom at the same time in late summer. Photoperiodism had made the small plants, which were planted late, flower at almost the same time as the large plants, planted much earlier.

There is much to learn about the ecological importance of photoperiodism. So far, responses of only a few hundred of the approximately three hundred thousand species of flowering plants have been studied. SEE ALSO CLINES AND ECOTYPES; HORMONAL CONTROL AND DEVELOPMENT; PHYTOCHROME; RHYTHMS IN PLANT LIFE.

Frank B. Salisbury

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Photorespiration

See Photosynthesis, Carbon Fixation and.

Photosynthesis, Carbon Fixation and

Virtually all life on Earth ultimately depends on the light-driven fixation of carbon dioxide (CO_2) according to the following equation:

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 \text{ (glucose)} + 6O_2$$

A micrograph of plant cell chloroplasts.

Photosynthesis takes place in subcellular membrane-bound compartments called **chloroplasts**. As radiotracers such as carbon-14 became available to researchers following World War II (1939–45), one application was to define the biochemistry of photosynthetic CO_2 fixation. Major class divisions in the plant kingdom are based on how CO_2 is fixed.

chloroplast the photosynthetic organelle of plants and algae

C_3 Photosynthesis. Many important biological processes are sustained by cycles that continuously consume and renew one or more key intermediates while producing some other major product. Photosynthesis is sustained by the Calvin-Benson cycle.

The C_3 photosynthetic mechanism is so named because the carbon atom of a molecule of CO_2 taken up by an illuminated leaf is first detected in the three-carbon **compound** 3-phosphoglyceric acid (PGA). The vast majority of higher plants and algae are C_3 species. PGA is formed when CO_2 combines with a 5-carbon sugar, ribulose biphosphate (RuBP). The reaction is catalyzed by the **enzyme** RuBP carboxylase/oxygenase, an abundant protein in all green tissues. This multifunctional enzyme has come to be called rubisco.

compound a substance formed from two or more elements

enzyme a protein that controls a reaction in a cell

During each turn of the Calvin-Benson cycle, two molecules of PGA (a total of six carbon atoms) undergo a complex series of enzyme-catalyzed transformations in which the carbon atoms pass through metabolite pools consisting of three-, four-, five-, six-, and seven-carbon sugar phosphates. These reactions regenerate RuBP, which then combines with CO_2 to form two PGAs and complete the cycle. So, of the six (2 H 3) original carbon atoms in PGA, five give rise to RuBP and the one remaining appears as one of the six carbon atoms in the sugar glucose-6-phosphate (G6P). Therefore, for every six CO_2 molecules fixed, one G6P leaves the Calvin-Benson cycle for synthesis of starch, sucrose, cellulose, and ultimately all of the organic constituents of the plant.

In terms of pure chemistry, the conversion of CO_2 to carbohydrate is an example of reduction, in which a source of energy-rich electrons is required. As the term *photosynthesis* suggests, the energy for the reductive reactions of the Calvin-Benson cycle comes from visible light. An extensive membrane system in the chloroplast harbors the **pigments** (chlorophylls and carotenoids) that transfer light packets (quanta) to specialized pigment-protein sites where they energize individual electrons extracted from molecules of water (H_2O). The oxygen atoms in the water are released as O_2. Each high-energy electron consumes the energy of two quanta. Two electrons are used to convert a compound called nicotinamide adenosine dinucleotide phosphate from its oxidized form ($NADP^+$) to its reduced form (NADPH). The sequence of electron transport from H_2O to $NADP^+$ also fuels the phosphorylation of adenosine diphosphate (ADP) to high-energy adenosine triphosphate (**ATP**). Both NADPH and ATP interact directly with the enzymes of the Calvin-Benson cycle during fixation of CO_2. Two molecules of NADPH and three molecules of ATP are required to fix each molecule of CO_2 during C_3 photosynthesis.

pigments colored molecules

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

Photorespiration. C_3 plants also engage in an active CO_2-releasing process called photorespiration that operates concurrently with normal photosynthesis in the light. Photorespiration drains away useful energy, and is thus a wasteful process. Since the CO_2 formed by photorespiration is rapidly refixed by photosynthesis it is difficult to measure directly, and its existence was not suspected until the 1950s. Since then, biochemists and physiologists have elucidated the mechanism, but have not come to agreement on its purpose, if any. It is important to note that photorespiration is not the same as the ubiquitous respiratory CO_2 released from **mitochondria** in all **eukaryotic** cells, including animal and plant tissues.

mitochondria cell organelles that produce ATP to power cell reactions

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

Photorespiration starts with the formation of a two-carbon phosphoglycolic acid molecule during photosynthesis. Since this is a potent inhibitor of the Calvin-Benson cycle, its metabolism to nontoxic derivatives is essential. First, the phosphate group is removed (by action of an enzyme called a phosphatase) to yield glycolate. The following series of conversions:

2 glycolate → 2 glyoxylate → 2 glycine → serine → hydroxypyruvate → PGA

results in the formation of a Calvin-Benson cycle intermediate (PGA) that is used to make RuBP. Notice that the four glycolate carbon atoms ultimately appear as one molecule of PGA (three carbon atoms). The fourth atom of carbon is released as CO_2 during the glycine to serine conversion, and this is the source of CO_2 released in photorespiration. Additional photosynthetic energy (i.e., NADPH and ATP) is consumed during metabolism of photorespiratory PGA, refixation of CO_2, and reassimilation of ammonia released during the glycine→serine step. Hence, photorespiration drains energy away from productive photosynthesis.

Photorespiration can be observed by a number of means. When a stream of CO_2-free air is passed over a C_3 leaf, release of CO_2 by the leaf results

in an elevated concentration of this gas in the downstream flow. This release rate is highly dependent upon illumination of the leaf and will be depressed severalfold by darkening. Another method relies on the fact that the rate of photosynthetic fixation of CO_2 is directly dependent on the concentration of CO_2 at low levels of this component. Hence, sealing a leaf in a small transparent vessel under illumination will cause the concentration of CO_2 inside to fall until the rate of uptake equals the rate of evolution due to photorespiration. The final equilibrium concentration of CO_2 (called the CO_2 compensation point) is highly dependent on the concentration of O_2 in the gas and is commonly employed as a robust, although indirect, measure of photorespiration. But the most direct indicator of photorespiration is based on comparison of rates of CO_2 uptake at high and low levels of O_2 in the surrounding atmosphere. Lowering the O_2 concentration from the normal 21 percent to 1 to 2 percent can result in an instantaneous 30 percent increase in photosynthetic rate (see below). This response of photosynthesis to O_2 is attributed to photorespiration and is called the Warburg Effect for its discoverer Otto Warburg.

Although the source of phosphoglycolic acid for photorespiration was for some time a controversial subject, it is now widely accepted that it originates at the site of CO_2 fixation. Specifically, when RuBP binds to rubisco its structure is perturbed, rendering it vulnerable to attack by either CO_2 or O_2. Reaction of RuBP with CO_2 yields two PGAs while reaction with O_2 results in formation of one PGA molecule and one phosphoglycolic acid molecule. The probability that a bound RuBP will react with either CO_2 or O_2 is governed by the relative concentrations of these gases in the aqueous environment of the chloroplast. Hence, CO_2 and O_2 are considered to compete for the bound RuBP. This competition accounts for the increase in photorespiration at high O_2 concentration, and the fact that photorespiration can be almost completely suppressed by high concentrations of CO_2 even in the presence of O_2. Measurements with purified rubisco in the laboratory indicate that the rate of photorespiratory release of CO_2 is about 20 percent of the total rate of CO_2 uptake for a healthy C_3 leaf in air at 25°C. Photorespiration increases considerably with temperature, however. Photorespiration is most significant when temperatures are high and plants must close **stomata** to prevent water loss. Without access to fresh CO_2 from the atmosphere, photorespiration becomes the major reaction catalyzed by rubisco.

stomata openings between guard cells on the underside of leaves that allow gas exchange

The role of photorespiration in plant metabolism is the subject of debate. It has been suggested to be a means of disposal of excess photosynthetic energy. Also, it may provide a way to protect the leaf from damaging effects of light that could occur if CO_2 levels inside the leaf were to fall below some critical threshold. Still, there may be no essential role for photorespiration. It is probably an anomaly of the rubisco mechanism that appeared on this planet before O_2 was present in the atmosphere. Later, as O_2levels in the atmosphere rose due to photosynthesis, this vulnerability to O_2 affected photosynthesis and growth. Interestingly, some plants have evolved means to suppress photorespiration while retaining rubisco and the Calvin-Benson cycle.

C_4 Photosynthesis. Familiar species possessing the C_4 photosynthesis mechanism are maize, sorghum, sugarcane, and several common weeds. The defining feature of CO_2 fixation in this case is involvement of two distinct cell types that shuttle metabolites back and forth to complete a modified photosynthetic cycle. Microscopic examination of leaf sections reveals two chloroplast-containing cell types in an arrangement termed Kranz anatomy. Bundle sheath cells form a cylindrical layer one cell deep around each leaf vein. These cells are typically enlarged, thick walled, and densely packed with chloroplasts. At least two layers of loosely packed mesophyll cells separate adjacent bundle sheath strands. Although mesophyll cells resemble those observed in C_3leaves, they function much differently.

When CO_2 enters the leaf it is first fixed in the mesophyll cells by the enzyme phosphoenolpyruvate (PEP) carboxylase. The carbon atom from CO_2 is first detected in the four-carbon organic acid oxaloacetic acid (OAA), hence the name C_4 photosynthesis. The OAA is then reduced to malic acid or converted to the amino acid aspartic acid depending on species. Malate and aspartate are transported to bundle sheath cells where they are decarboxylated, thereby releasing CO_2. This newly formed CO_2 is refixed by rubisco and metabolized by the Calvin-Benson cycle present in the bundle sheath chloroplasts. The remaining three carbon atoms derived from the malate and aspartate are transported back to the mesophyll cells as pyruvic acid to regenerate the three-carbon PEP.

The characteristic carboxylation/decarboxylation sequence of C_4 photosynthesis pumps CO_2 from mesophyll to bundle sheath cells, thereby accomplishing one desirable end. The concentration of CO_2 in bundle sheath cells of C_4 plants is severalfold higher than in leaf cells of C_3 species. Hence, photorespiration is virtually absent in C_4 leaves. Since none of the other enzyme-catalyzed reactions is sensitive to O_2, the Warburg effect is not observed and the CO_2 compensation point (a reliable indicator of photorespiratory capacity, see above) is very low for C_4 leaves. Somewhat more light energy is required to fix each molecule of CO_2 using the C_4 pathway since PEP regeneration requires ATP. Although 2 NADPH are consumed as in C_3 plants, the ATP requirement for C_4 photosynthesis is four to five per CO_2 fixed.

Crassulacean Acid Metabolism (CAM). The crassulacean acid metabolism (CAM) mode of photosynthesis was discovered first in plants of the family Crassulaceae but familiar species include pineapple and cacti. It is considered an adaptation to life in arid environments. CAM photosynthesis resembles C_4 photosynthesis in terms of the pathway of fixation of carbon. The prominent difference, however, is that CAM plants take up CO_2 from the atmosphere at night and synthesize malic acid via PEP carboxylase. During the daytime the leaf pores (stomata) that admit CO_2 close to conserve water. Malic acid is decarboxylated and the CO_2 is refixed by the Calvin-Benson cycle. Some of the starch accumulated during daytime is converted to PEP at night to support CO_2 fixation. Also, unlike C_4 photosynthesis, all of the CAM reactions take place in each leaf cell.

Significance of Carbon Fixation Reactions

The choice of CO_2 fixation pathway has profound implications for how a plant responds to the innumerable combinations of light intensity, leaf internal CO_2 concentration, temperature, and water status in the natural environment. As discussed above, at normal atmospheric CO_2 levels photosynthesis is lower by at least 25 percent in C_3 plants than it would be if photorespiration were absent. The generally higher rates of photosynthesis in C_4 plants are attributable to both suppression of photorespiration in these species and the superior ability of PEP carboxylase to fix CO_2 at the very low concentrations of this gas that can occur inside leaf tissue. These differences are most pronounced at high light intensity. Photosynthesis in C_3 leaves attain maximal rates at light levels of about 50 percent of full sunlight. However, C_4 photosynthesis continues to increase with light intensity even in full sunlight. It is little wonder that the highest yielding crop species use the C_4 mechanism. Conversely, C_3 plants are capable of more efficient use of light quanta when light levels are low, as would be the case for shaded conditions. Also, high temperatures favor C_4 plants because the number of molecules of H_2O lost to evaporation via the stomata (transpiration) per CO_2 fixed is much lower for these species compared to C_3 species. However, C_3 plants tend to be more competitive in cool environments. Finally, although projected increases in global atmospheric CO_2 levels during the twenty-first century should enhance photosynthesis in all species, associated changes in distribution of temperature and rainfall will also exert great influence on the composition and characteristics of Earth's flora. SEE ALSO ATMOSPHERE AND PLANTS; CACTUS; CALVIN, MELVIN; CHLOROPLAST; DE SAUSSURE, NICHOLAS; INGENHOUSZ, JAN; PHOTOSYNTHESIS, LIGHT REACTIONS AND.

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Photosynthesis, Light Reactions and

Life requires a continuous input of energy. On Earth, the main source of energy is sunlight, which is transformed by photosynthesis into a form of chemical energy that can be used by photosynthetic and nonphotosynthetic organisms alike. Photosynthesis is the molecular process by which plants, algae, and certain bacteria use light energy to build molecules of sugar from carbon dioxide (CO_2) and water (H_2O). The sugar molecules produced by photosynthetic organisms provide the energy as well as chemical building blocks needed for their growth and reproduction. In plants and algae the photosynthetic process removes CO_2 from the atmosphere while releasing molecular oxygen (O_2) as a by-product. Some photosynthetic bacteria function like plants and algae, giving off O_2; other types of photosynthetic bacteria, however, use light energy to create organic **compounds** without producing O_2. The type of photosynthesis that releases O_2 emerged early in

compound a substance formed from two or more elements

Earth's history, more than three billion years ago, and is the source of the O_2 in our atmosphere. Thus photosynthetic organisms not only provide the food we eat, but also the air we breathe. In addition, ancient photosynthesis produced the building blocks for the oil, coal, and natural gas that we currently depend on for our survival.

The overall photosynthetic process can be written as:

Carbon Dioxide + Water + Light → Carbohydrate + Oxygen

and can be summarized by the following chemical equation:

$$6\ CO_2 + 6\ H_2O + \text{Light Energy} \rightarrow (CH_2O)_6 + 6\ O_2$$

However, this simple chemical equation does not reveal all the reactions that must occur inside a plant to produce carbohydrate. If you shine light on a mixture of CO_2 and H_2O, you end with what you started, CO_2 and H_2O. Add a plant, however, and you get sugar. Plants create this sugar in a series of molecular steps using a complicated machinery made up of proteins and other organic molecules.

This article describes the photosynthetic process in plants, focusing on the first stage of photosynthesis, known as the light reactions. The light reactions capture light energy and store it within two chemicals, **NADPH** (nicotinamide adenine dinucleotide phosphate) and **ATP** (adenosine triphosphate). These two molecules provide the energy needed to drive the second stage of photosynthesis, known as the Calvin-Benson cycle, in which carbohydrates (sugars) are made from CO_2 and H_2O.

NADPH reduced form of nicotinomide adenine dinucleotide phosphate, a small, water-soluble molecule that acts as a hydrogen carrier in biochemical reactions

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

ions charged particles

To perform photosynthesis a plant must gather light energy, transport electrons between molecules, transfer protons across a membrane, and finally rearrange chemical bonds to create carbohydrates. To understand the light reactions it is helpful to focus on the path of three critical elements: energy, electrons, and protons (hydrogen **ions**). However, before considering the series of individual reactions that make up the light reactions, the molecular machinery that does all the work must be examined.

Chloroplasts

organelle a membrane-bound structure within a cell

enzyme a protein that controls a reaction in a cell

vesicle a membrane-bound cell structure with specialized contents

In plants and algae, photosynthesis occurs in chloroplasts, which are small **organelles** located inside cells. The chloroplast can be thought of as a factory, providing the plant with food and energy. A typical cell in a leaf contains many chloroplasts. Fortunately chloroplasts from different plants are more similar than different. This means that if you understand how photosynthesis works in one plant, you will have a general understanding of photosynthesis in all plants. The chloroplast contains a membrane system, known as the photosynthetic membrane (or thylakoid membrane), that contains most of the proteins required for the light reactions. The Calvin-Benson cycle **enzymes** that capture CO_2 and produce carbohydrate are located in the water phase of the chloroplast outside the photosynthetic membrane. The photosynthetic membrane, like other cellular membranes, is composed mainly of lipid molecules arranged in a bi-layer. As will be explained, a critical feature of the photosynthetic membrane is that it forms a **vesicle** that defines an inner and an outer water space. The photosynthetic membrane is organized into stacked membranes that are interconnected by nonstacked membranes. Researchers are uncertain as to why the photosynthetic membrane is organized in such a complicated structure. Fortunately, to understand the photosynthetic light reactions we can represent the shape of the photosynthetic membrane as a simple vesicle.

Gathering Sunlight: The Antenna System

Plants capture sunlight by using pigment molecules that absorb visible light (wavelengths from 400 to 700 **nanometers**). The main light-absorbing molecule is chlorophyll, which gives plants their green color. Chlorophyll is green because it is efficient at absorbing blue light and red light, but not very efficient at absorbing green light. The chlorophyll and other light-absorbing molecules (for example, **carotenoids**, which are yellow) are bound to protein complexes embedded in the photosynthetic membrane that make up an **antenna system**. This antenna system is designed to absorb light energy and funnel it to a protein complex called a **reaction center**. The reaction center can use the energy to drive an electron uphill from one site to another within the reaction center. Each reaction center is located at the center of the antenna system, which contains two hundred to three hundred chlorophyll molecules. Before the first chemical step can take place, the light energy captured by the antenna system must be transferred to the reaction center.

nanometer one-billionth of a meter

carotenoid a yellow-colored molecule made by plants

antenna system a collection of protein complexes that harvests light energy and converts it to excitation energy that can migrate to a reaction center. The light is absorbed by pigment molecules (e.g., chlorophyll, carotenoids, phycobilin) that are attached to the protein

reaction center a protein complex that uses light energy to create a stable charge separation by transferring a single electron energetically uphill from a donor molecule to an acceptor molecule, both of which are located in the reaction center

To understand light absorption it is best to think of light as packets of energy known as photons. The job of the antenna system is to capture photons and change the light energy into another form of energy known as excitation energy, which is a type of electronic energy. The excitation energy can be thought of as a packet of energy that jumps from antenna molecule to antenna molecule until it is trapped by a reaction center. The antenna system is very efficient. Under optimum conditions more than 90 percent of the photons gathered by the antenna system are transferred to the reaction center. The migration of excitation energy in the antenna system is also very fast. A photon is absorbed, transferred around the antenna system, and trapped by a reaction center within a few trillionths of a second (10^{-12} s).

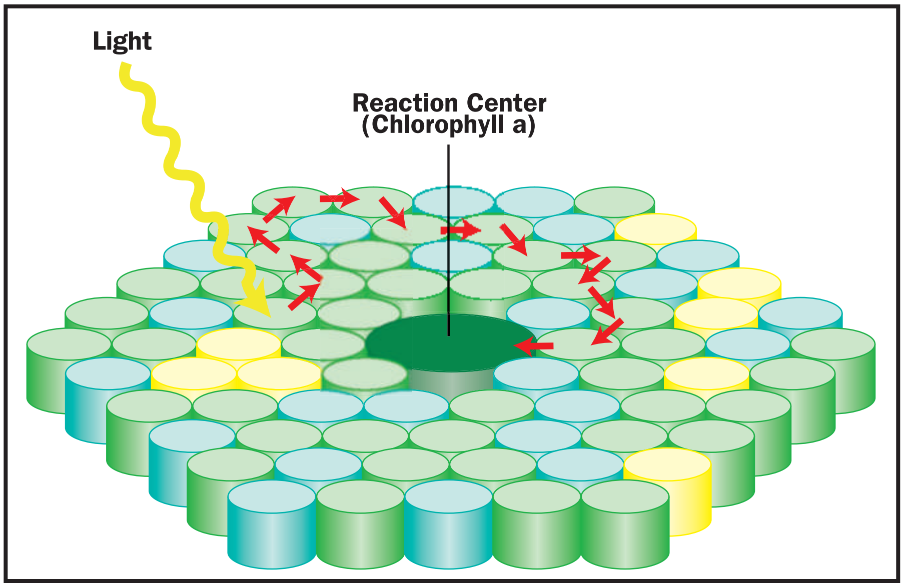

Figure 1: Antenna system with a reaction center (middle). The arrows indicate the pathway of excitation energy migration. Redrawn from Starr and Taggart, 1998, Figure 7.9.

Electron Transport

$NADP^+$ oxidized form of nicotinomide adenine dinucleotide phosphate

The excitation energy trapped by a reaction center provides the energy needed for electron transfer, which is the next step in the photosynthetic light reactions. During electron transfer, individual electrons are removed from water molecules and transferred, by an electron transport chain, to **$NADP^+$**. Electron transport in photosynthesis is like electron flow in an electric circuit driven by a battery. The voltage difference across the battery pushes electrons through the circuit, and the electron current can be used to do work. In photosynthesis, light energy pushes electrons up an energy hill in the reaction centers. Subsequent electron flow in the electron transport chain is energetically downhill and can be used to do work. Figure 2 shows the electron carriers that make up the photosynthetic electron transport chain in a way that reveals the relative electronic energy on the vertical scale. This is known as the Z-scheme. Note that a negative voltage corresponds to a higher energy, so that downhill electron flow is from the top to the bottom of the figure.

The electron transport pathway includes electron transfer from one site to another within a protein, as well as electron transfer from one molecule to another (Figure 3). Most of the electron carriers are located in the photosynthetic membrane, but a few (for example, $NADP^+$) are located in the water phase surrounding the membrane. It is important to keep in mind that the electron transport chain shown in the figure is repeated many times in each chloroplast. A typical chloroplast will contain more than a million electron transport chains.

Electron transfer from one molecule to another is possible because certain types of molecules can easily give up or receive electrons. Some electron carriers can give up and receive a single electron (e.g., plastocyanin), while others can accept or donate more than one electron (e.g., $NADP^+$

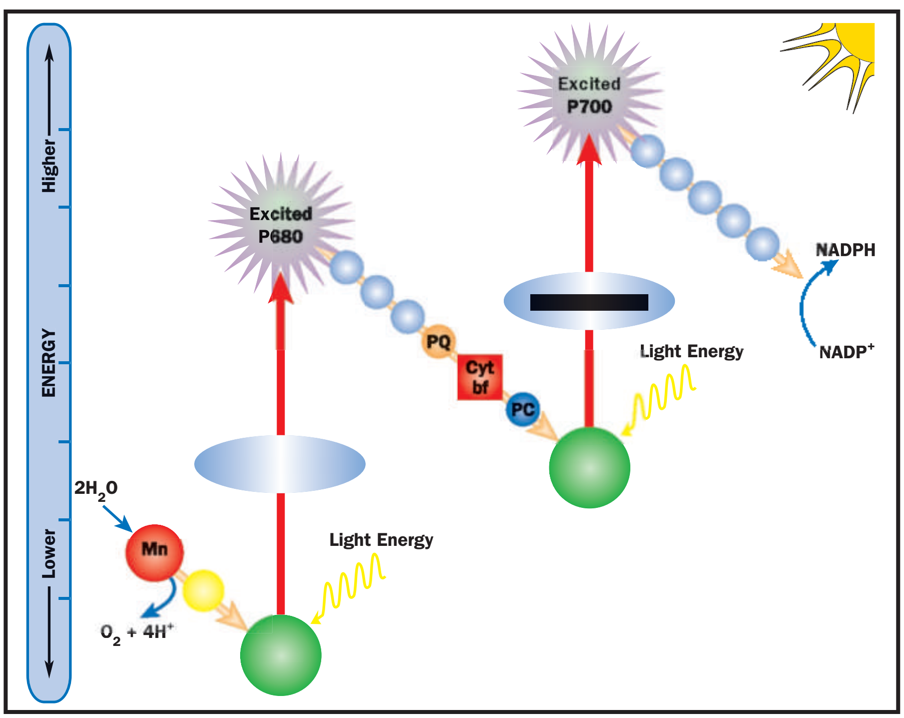

Figure 2: Z-scheme showing the pathway of electrons from water to $NADP^+$ producing oxygen and the reducing power (NADPH). Redrawn from www.life.uiuc.edu/govindjee/ZschemeG.html Mn = manganese; P680 = reaction center chlorophyll *a* of Photosystem II; PQ = plastoquinone; Cyt bf = cytochrome bf complex; PC = plastocyanin; P700 = reaction center chlorophyll of Photosystem I.

can accept two electrons). In addition, some electron carriers can take up a proton along with an electron (plastoquinone can accept two electrons and two protons), making them hydrogen (H) carriers.

When a compound gains an electron it is said to be *reduced* (**reduction**), whereas when it gives up an electron it is said to be *oxidized* (**oxidation**). In biological electron transport pathways, the electrons are always bound to a molecule (they are too reactive to hang around free), which means that an oxidation reaction is always coupled to a reduction reaction. Electrons spontaneously jump from one molecule to another because some molecules hold onto their electrons more tightly than others. This is another way of saying that energetically, electrons flow downhill. If two molecules, A and B, are close enough together, and if A is reduced and B is oxidized, an electron will jump from A to B if it is energetically downhill.

reduction the addition of one or more electrons to an atom or molecule. In the case of a molecule, protons may be involved as well, resulting in hydrogen being added

oxidation The removal of one or more electrons from an atom or molecule. In the case of a molecule, a proton may be involved as well, resulting in hydrogen being removed

NADPH Production

Moving an electron from water to $NADP^+$ requires an input of energy. This job is done by reaction centers, which use the light energy gathered by the antenna system to move an electron energetically uphill. As shown in Figure 3 the electron transport chain in chloroplasts uses two different types of reactions centers: Photosystem II and Photosystem I. (For historical reasons the reaction centers are not numbered according to their order in the electron transport chain, i.e., Photosystem II sends electrons to photosystem I.)

Photosystem II catalyzes two different chemical reactions. One is the oxidation of water and the other is the reduction of plastoquinone. Water oxidation is a critical reaction in photosynthesis because the electrons removed from H_2O are ultimately used to reduce CO_2 to carbohydrate. Photosystem II performs this reaction by binding two H_2O molecules and removing one electron at a time. The energy for the removal of a single electron is provided by a single photon. For Photosystem II to completely oxidize two H_2O molecules and reduce two molecules of plastoquinone, it requires four photons. (Note that electron transport from H_2O all the way to $NADP^+$ requires two light reactions: Photosystem II and Photosystem I. Thus eight photons are required for the release of one O_2 molecule.) This process creates O_2, which is released, and H^+ ions, which are used in ATP synthesis (see below).

As shown in Figure 3, electron transfer from water to $NADP^+$ requires three membrane-bound protein complexes: Photosystem II, the cytochrome *bf* complex (Cyt bf), and Photosystem I. Electrons are transferred between these large protein complexes by small mobile molecules. Because these small molecules carry electrons (or hydrogen atoms) over relatively long distances, they play a critical role in photosynthesis. This is illustrated by plastoquinone (PQ), which transfers electrons from the Photosystem II reaction center to the cytochrome *bf* complex and at the same time carries protons across the photosynthetic membrane.

Plastoquinone operates by diffusing in the photosynthetic membrane until it becomes bound to a pocket on the Photosystem II complex. The photosystem II reaction center reduces plastoquinone by adding two electrons taken from H_2O and two protons taken from the outer water phase, creating PQH_2. The reduced plastoqinone molecule unbinds from Photosystem II and diffuses in the photosynthetic membrane until it encounters a binding site on the cytochrome *bf* complex. In a reaction sequence that is

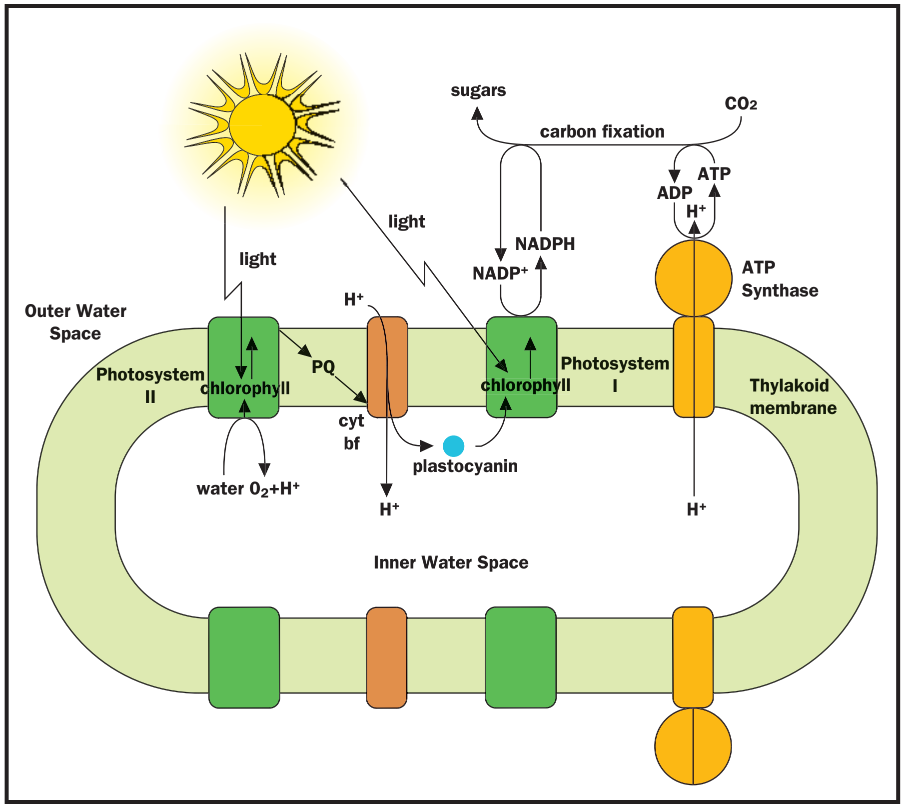

Figure 3: The electron transport chain showing the carriers in a membrane that forms a vesicle. Modified from photoscience.la.asu.edu/photosyn/education/photointro.html. See text for abbreviations used.

not completely understood, the cytochrome *bf* complex removes the electrons from reduced plastoquinone and releases protons into the inner water space of the photosynthetic vesicle. The cytochrome *bf* complex then gives up the electrons to another small molecule, plastocyanin (PC). The electrons are transferred to the Photosystem I reaction center by plastocyanin. The proton gradient, produced by water oxidation and oxidation of reduced plastoquinone, is used to create ATP (see below).

The Photosystem I reaction center is like Photosystem II in that it is served by a chlorophyll-containing antenna system and uses light energy to move an electron energetically uphill, but Photosystem I catalyzes different reactions: it oxidizes plastocyanin and reduces ferredoxin. Ferredoxin itself becomes oxidized, losing its electrons to another acceptor. The last step in the photosynthetic electron transport chain is reduction of $NADP^+$, producing NADPH.

ATP Production

In plants essentially all electron flow from water follows the pathway shown in Figure 3, at least up to ferredoxin. However, once an electron reaches ferredoxin the electron pathway becomes branched, enabling a fraction of the **redox** free energy to enter other pathways, including cycling through the Photosystem I reaction center. Photosystem I cyclic electron transport provides additional energy for ATP production, which allows plants to adjust the energy flow according to their metabolic needs.

redox oxidation and reduction

Most of the energy from the electron transfer reactions is stored as redox energy in NADPH as described above. However, some of the energy is stored across the membrane of the photosynthetic vesicle in the form of a **pH** gradient (or protein gradient) and an electric potential (positive inside). As previously noted, the electron transport chain concentrates protons in the inner water phase of the vesicle by the release of protons during the oxidation of water by Photosystem II and by transporting protons from the outer water phase to the inner water phase via plastoquinone (Figure 3). In addition, electron transport creates a net positive charge on the inner side and a net negative charge on the outer side of the vesicle, which gives rise to an electric potential across the membrane. The energy stored in the pH gradient and electric potential is known as the transmembrane proton electrochemical potential or the proton motive force.

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral; low pH numbers indicate high acidity; high numbers indicate alkalinity

The conversion of proton electrochemical energy into the chemical-free energy of ATP is accomplished by a single protein complex known as ATP synthase, which catalyzes the formation of ATP by the addition of inorganic phosphate (P_i) to ADP:

$$ADP + P_i \rightarrow ATP + H_2O$$

The reaction is energetically uphill and is driven by the transmembrane proton electrochemical gradient. The ATP synthase enzyme is a molecular rotary motor. Protons move through a channel in the ATP synthase pro-

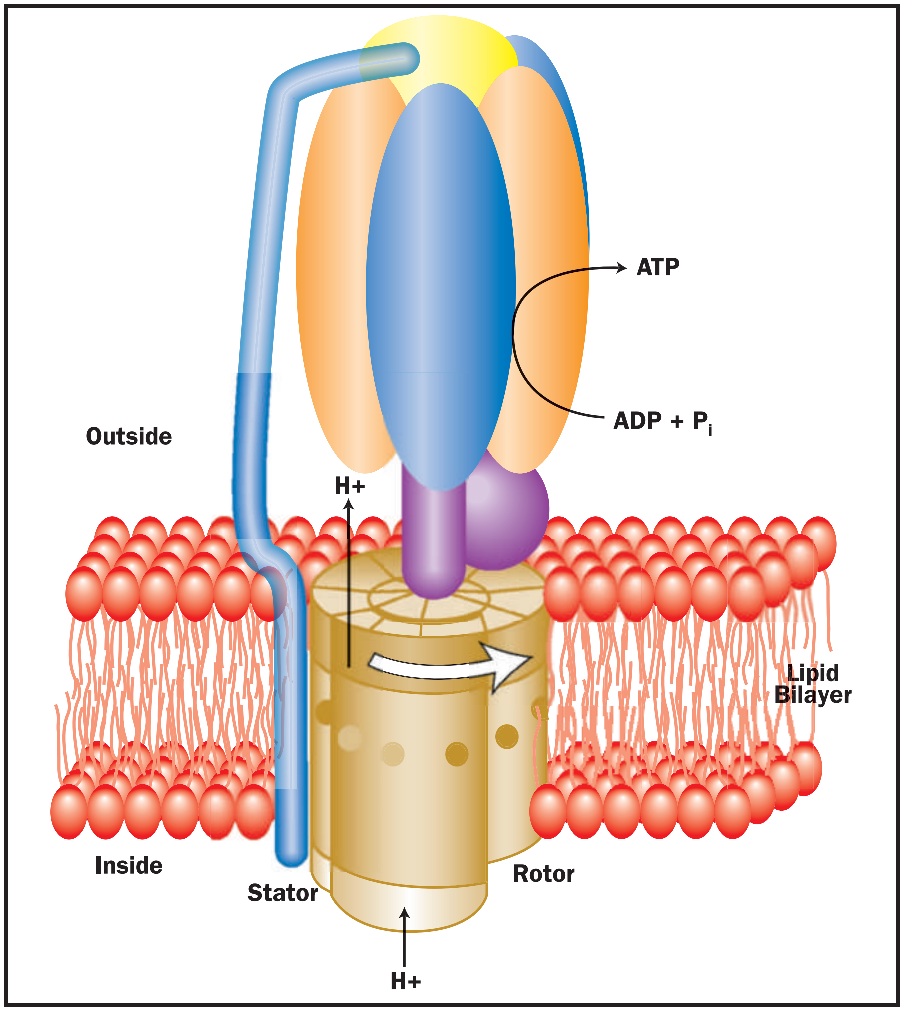

Figure 4: Rotary model of how ATP synthase catalyzes ATP. Redrawn from Fillingame, 1999, pp. 1687–88.

tein (from the inner water phase to the outer water phase of the vesicle) providing the energy for ATP synthesis. However, the protons are not involved in the chemistry of adding phosphate to ADP at the catalytic site. Although it has not been proven, it appears that proton flow drives the rotation part of the ATP synthase at rates as high as one hundred revolutions per second (Figure 4). The rotation of ATP synthase can be thought of as pushing ADP and P_i together to form ATP and water.

From the Light Reactions to the Calvin-Benson Cycle

The job of the photosynthetic light reactions is to provide energy in the form NADPH and ATP for the Calvin-Benson cycle. Although all plants depend on the Calvin-Benson cycle to make carbohydrates, the way they get the carbon dioxide to the cycle varies. The most efficient plants (soybean, for example) require two molecules of NADPH and three molecules of ATP for each molecule of CO_2 that is taken up, while some other types of plants (corn, for example) must use more energy to fix a single CO_2 molecule. During brief periods photosynthesis in plants can store nearly 30 percent of the light energy they absorb as chemical energy. However, under normal, day-to-day growing conditions the actual performance of the plant is less than one-tenth of the maximum efficiency. The factors that conspire to lower photosynthesis include limitations imposed by molecular reactions and environmental conditions that limit plant performance such as low soil moisture or high temperature. Our increasing understanding of plant **genomes** opens the door for improving plant performance under diverse environmental conditions (for example, enabling farmers to grow crops on marginal lands). A crucial step in this direction is understanding the molecular processes involved in photosynthesis. SEE ALSO CHLOROPHYLL; CHLOROPLASTS; INGENHOUSZ, JAN; PHOTOSYNTHESIS, CARBON FIXATION AND; WATER MOVEMENT.

genome the genetic material of an organism

John Whitmarsh and Govindjee

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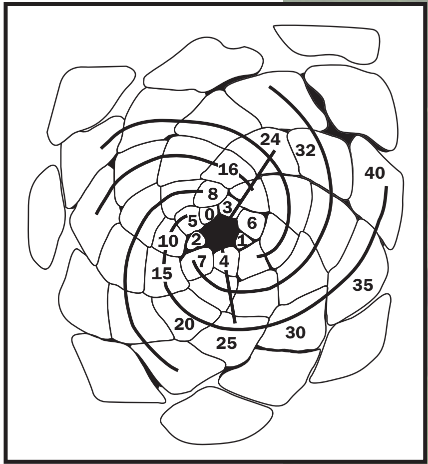
Phyllotaxis

Phyllotaxis is the study of the patterns on plants. The word itself comes from the Greek *phullon*, meaning "leaf," and *taxis*, meaning "arrangement." Phyllotaxis, in the restricted sense, is the study of the relative arrangement of what is called the primordia of plants. A primordium is, for example, what will become a leaf on a stem, a scale on a pinecone or on a pineapple fruit, a seed in the head (called the **capitulum**) of a sunflower, or a floret in the capitulum of a daisy. In other words, phyllotaxis is the study of the patterns made by similar parts (such as florets, scales, and seeds) on plants and in their buds. Anatomically, phyllotactic patterns are closely related to the **vascular** systems of plants, but phyllotaxis-like patterns are even present in the brown alga *Fucus spiralis*, in which there is no vascular system. The study of phyllotaxis has brought about new ideas and considerable progress in our knowledge of the organization of vegetative shoots. Phyllotaxis was the oldest biological subject to be mathematized, well before genetics.



Cross-section of an apical bud of *Pinus pinea,* with five parastichies in one direction and eight in the opposite direction.

capitulum the head of a compound flower, such as a dandelion

vascular related to transport of nutrients

apical at the tip

Types of Phyllotaxis

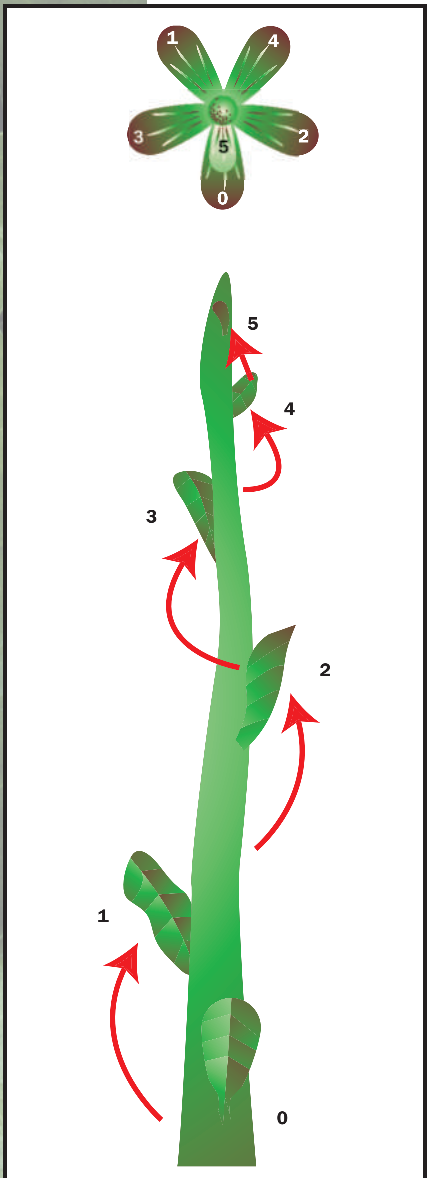
In the mid-1830s naturalists noticed the spirals in the capituli of daisies and sunflowers. There are indeed two easily recognizable families of spirals, winding in opposite directions with respect to a common pole that is the center of the capitulum. They also noticed the patterns of scales making families of spirals on the pineapple fruit surface. Depending on whether the scales are rectangular or hexagonal, there are two or three such families of spirals or helices that can be easily observed. These spirals are referred to as parastichies, meaning "secondary spirals." The accompanying figure of the *Pinus pinea* shows a cross-section of an **apical** bud with five parastichies in one direction and eight in the opposite direction. Similar patterns of helices are made by the points of insertions of the leaves around stems, such as the patterns of scars made by the leaves on the trunk of a palm tree.

Apart from the spiral or helical pattern, which is the type most frequently encountered in nature, there is another main type of phyllotaxis called whorled. A pattern is whorled when *n* primordia appear at each level of the stem, such as in horsetails (*Equisetum*), in which *n* can take values from 6 to 20. When the *n* primordia on a level are inserted in between those of the adjacent level, the **whorl** is said to be alternating, as in fir club moss (*Lycopodium selago*). When they are directly above those in the adjacent level, the whorl is called superposed, as in *Ruta* and *Primula*.

whorl a ring

Numbers in Phyllotaxis

In the case of the spirals in the capitulum of the daisy, or in the case of those in the cross-section of the young pine cone in the figure, the spirals are often conceived as logarithmic spirals. In the case of mature pinecones and stems they are helices made by scales winding around a cylinder-like form. When naturalists count the spirals they find that in 92 percent of all the observations, the numbers of spirals are terms of the Fibonacci sequence, named after Leonardo Fibonacci, the most famous mathematician of the twelfth century. It is also called the main sequence. This is the recurrent sequence 1, 1, 2, 3, 5, 8, 13, 21, 34, . . . where each term is the sum of the preceeding two. The next terms are thus 55 and 89, and the three dots (. . .) indicate that the sequence is infinite. Still more fascinating and puzzling is the fact that the number of spirals are consecutive terms of the Fibonacci sequence. For example, in the pine we have (2, 3), (5, 3), and (5, 8) phyllotaxes, in capituli the pairs found are (21, 34), (55, 34), (55, 89), and (89, 144), and on pineapples with hexagonal scales the triplets (8, 13, 21) or (13,



A leafy stem showing a divergence angle, between consecutively borne leaves, of 2/5 of a turn around the stem (144 degrees).

specimen object or organism under consideration

21, 34) are found, depending on the size of the **specimens**. The prevalence of the Fibonacci sequence in phyllotaxis is often referred to as "the mystery of phyllotaxis."

There are, of course, exceptions to the rule, but in the other cases of spiral (as opposed to whorled) phyllotaxis, the numbers obtained are consecutive terms of a Fibonacci-type sequence. This is a sequence of integers built on the same recurrence relationship as for the Fibonacci sequence, but starting with numbers different from 1 and 1, for instance: 1, 3, 4, 7, 11, 18, 29. . . . This sequence, encountered in *Araucaria* and *Echinocactus*, is present in about 1.5 percent of all observations, while the sequence 2, 2, 4, 6, 10, 16, 26 (the double Fibonacci sequence called the bijugate sequence) arises in around 6 percent of all the cases and is observed for example in *Aspidium* and *Bellis*. The phenomenon of phyllotaxis is thus essentially simple as far as those sequences are concerned, but the matter becomes complicated when on the same plant, such as *Bryophyllum* and *Anthurium*, one observes many Fibonacci-type sequences. This phenomenon is referred to as discontinuous transition. In the capituli of sunflowers and daisies, transitions are made along the same sequence. For example, we can observe in the center of the head (5, 8) phyllotaxis, followed in the middle part by (13, 8) phyllotaxis, and in the outer part by (13, 21) phyllotaxis. This is called a continuous transition. This phenomenon of growth has to do with the way crystals grow, and the daisy can be considered a living crystal.

Stems of Leaves and the Golden Number. Let us consider now a stem of leaves, as naturalists did in the mid-1830s. Take a point of insertion of a leaf at the bottom of the stem, and, in a helical or spiral movement around the stem, go to the next leaves above by the shortest path from one leaf to the next until a leaf is reached that is directly above the first chosen one. The leaves are then linked consecutively (1, 2, 3, 4, 5, . . .) along a helix, while in the case of the pine cone in the figure the five parastichies link the primordia by steps of five (e.g., 0, 5, 10, 15, 20, . . .). Then by making the ratio of the number of turns around the stem to the number of leaves met, excluding the first one, we obtain a fraction, such as 2/5, illustrated in the accompanying figure of the stem. In a significant number of cases the fractions obtained on various stems are 1/2, 1/3, 2/5, 3/8, 5/13, 8/21. . . . The numerators and the denominators of this sequence of fractions are consecutive terms of the Fibonacci sequence. Each fraction represents an angle d between two consecutive leaves along the helix, known as the divergence angle. In the case of the pine cone the divergence is the angle between consecutively numbered primordia such as #24 and #25, and using a protractor it can be checked that $d \cong 137.5$ degrees, which is known as the Fibonacci angle.

These divergences are closely related to what is known as the golden number, denoted by the Greek letter τ (tau), where $\tau \cong 1.618$. Indeed, the value of $1/\tau^2 \cong 0.382$, which is the value the sequence of fractions approaches. For example, $5/13 \cong 0.384$ or $8/21 \cong 0.380$, and as we take fractions farther away in the sequence, such as 21/55, we find that $21/55 \cong 0.381$ and that we are gradually approaching the value of $1/\tau^2$. Also the value of $360/\tau^2 \cong 137.5$.

Phyllotaxis and Explanatory Modeling. The aim of explanatory modeling is to try to reproduce the patterns from rules or mechanisms or principles—

imagined or hypothesized by the modeler—that are considered to be in action in shoot apices. The hypotheses are then transcribed into mathematical terms and their consequences are logically drawn and compared to reality. Two old hypotheses in particular have been scrutinized in different manners by the modelers. One is the chemical hypothesis that a substance such as a plant hormone produced by the primordia and the tip of the apex is at work, inhibiting the formation of primordia at some places and promoting their formation at others, thus producing the patterns. Another stresses the idea that physical-contact pressures between the primordia generate the patterns. A new hypothesis suggests that elementary rules of growth such as branching, and elementary principles such as maximization of energy, are at work producing the patterns. This model predicts the existence of a very unusual type of pattern, known as monostichy, in which all the primordia would be superimposed on the same side of the stem. This type of pattern was later discovered to exist in *Utricularia*. The same model shows the unity behind the great diversity of patterns.

Phyllotaxis is clearly a subject at the junction of botany and mathematics. Mathematics helps to organize the data, give meaning to it, interpret it, and direct attention to potentially new observations. The study of phyllotaxis has become a multidisciplinary subject, involving general comparative morphology, paleobotany, genetics, molecular biology, physics, biochemistry, the theory of evolution, **dynamical system theory**, and even **crystallography**. The patterns observed in plants can be seen to a much lesser extent in other areas of nature. SEE ALSO Anatomy of Plants; Leaves; Shape and Form of Plants; Stems.

Roger V. Jean

dynamical system theory the mathematical theory of change within a system

crystallography the use of x-rays on crystals to determine molecular structure

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Phylogeny

Before the mid-1800s, classification of organisms into groups, called **taxa**, was generally based on overall similarity of physical appearance. There was no guiding principle as to why the members of one group were more similar to each other than to the members of other groups. In 1859, Charles Darwin's *Origin of Species* was published, and Darwin's theory of evolution provided the explanation that natural groups occur because the members of the group are the descendants of a common ancestor. Based on Darwin's principles, in 1866, the German naturalist, Ernst Haeckel, coined the term *phylogeny* to describe the "science of the changes in form through which the phyla or organic **lineages** pass through the entire time of their discrete existence." Today the term phylogeny is used more widely to mean the evolutionary history or exact genealogy of a species or group of organisms. Phylogenies are based on the study of fossils, morphology, comparative anatomy, ultrastructure, biochemistry, and molecules.

taxa a type of organism, or a level of classification of organisms

lineage ancestry; the line of evolutionary descent of an organism

"PRIMITIVE" VS. "ADVANCED" CHARACTERS

Fossil evidence has shown that bryophytes are the most primitive of the extant land plants. Bryophytes lack true xylem and phloem, although some mosses and liverworts have conducting tissues. Therefore, the absence of true xylem and phloem is a primitive feature. The presence of well-developed vascular tissue (xylem and phloem) in gymnosperms and angiosperms is a derived character.

Similarly, gymnosperms lack vessels in the xylem and angiosperms have vessels. The fossil record tells us that the gymnosperms came first, therefore, we know the vessels are a more recent, or derived, character. Often it is the fossil record that helps scientists polarize characters. For those plants for which we do not have an adequate fossil record, such as many of the green algae, polarizing characters and constructing a phylogeny becomes more difficult.

monophyletic a group that includes an ancestral species and all its descendants

Theoretical Foundations

In his explicit phylogenetic scheme for land plants, Haeckel rejected theories of multiple origins for organisms, which he called polyphyletic. He used the term monophyly to describe a natural group of two or more taxa whose members are all descended from the nearest common ancestor. Phylogenies are based on **monophyletic** groups. The taxonomic theory of phylogenetic systematics is organized around the principles that organisms are related through descent from a common ancestor, that there are natural groups of monophyletic taxa, and that unique changes or modifications shared by members of a taxon are evidence of their evolutionary history.

Although monophyletic taxa exist in nature whether they are discovered or not, the goal of phylogenetic systematics is to reveal natural groups of taxa. The main principle of phylogenetic systematics is that natural groups are defined by uniquely shared evolutionary novelties, or homologous characters. A character is a heritable feature (one that is passed from an ancestor to its descendants) of an organism that can be described, measured, or otherwise compared to other organisms. To be considered homologous, a character must be not only heritable, but also independent from any other characters in an organism. The different forms a character may take are called the character states.

Similarities and Phenetic Systems

Systems of classification that are based on overall similarity are called phenetic systems. Phenetic classification schemes do not distinguish between homologous characters (where taxa share a similar characteristic because they inherited it from a common ancestor) and analogous characters (where the characteristic shared by taxa was not inherited from a common ancestor). Sharing of homologous characters is evidence that taxa are evolutionarily related. For instance, the phloem that is found in carnations, roses, and lilies is a homologous similarity because all of these plants inherited the character from a common ancestor. The analogous phloemlike conducting tissue found in the giant kelps off the coast of California is functionally similar to phloem, but not inherited from the same common ancestor as the flowering plants. The evolution of analogous characters is also known as convergence or homoplasy, and often is the result of similar selection pressures in the environment on different organisms. In phylogenetic analysis, characters that are not recognized as being analogous can lead to unreliable results.

A homologous character can be an ancient retained feature, known as a plesiomorphy; while a homologous character that is the result of more recent evolutionary modifications is termed a derived character, or apomorphy. If taxa have the same apomorphy (that is, they share the same derived character), the character is termed a synapomorphy. German entomologist Willi Hennig, whose work was first translated into English in 1966, argued that only these shared, derived homologous characters (synapomorphies) could provide information about phylogeny, the evolutionary relationships of organisms. The methodology Hennig proposed to group taxa that share derived characters is now called cladistics.

The Rise of Cladistics

Cladistic analysis is designed to find evidence about which two taxa are more closely related to each other than either is to a third. Finding this evidence requires distinguishing between primitive and derived states of a character, a process known as determining character polarity. The most widely used method for determining character polarity is the outgroup method.

The outgroup method is comparative. If a group of organisms being compared (the in-group) shares a character state with organisms outside the group (the outgroup), then the character state is considered to be plesiomorphic, and this character provides no information about relationships among the in-group taxa. For instance, as in the example above, phloem is found in carnations, roses, and lilies (the in-group). Phloem is also found, however, in pine trees (the outgroup), and, therefore, in this instance the presence of phloem is plesiomorphic. These comparisons are also relative. The presence of phloem is considered apomorphic (and informative) when used as evidence of monophyly in higher plants, because although phloem is found in all higher green plants, it is not found in the lower green plants, such as green algae or bryophytes.

In cladistics, these hierarchical relationships are shown on a branching diagram that is called a cladogram (sometimes referred to as an evolutionary tree). Taxa that share many homologues will group together more closely on a cladogram than taxa that do not. All of the taxa on each branch of a cladogram are considered to form a monophyletic group, comprising of all the descendants of a common ancestor plus that ancestor. This group is also known as a clade. Clades that are next to each other on a cladogram are known as sister clades and the taxa in the clades as sister taxa.

Cladistic methodology is based on a type of logical reasoning called parsimony. The principle of parsimony states that of two hypotheses, the one that explains the data in the simplest manner, or with the smallest number of steps, is best. Looking again at the example of presence of phloem, the hypothesis that carnations, roses, and lilies all have phloem because they inherited it from a single common ancestor requires fewer evolutionary steps and is therefore more parsimonious than the hypothesis that phloem arose two or three separate times.

Phylogeny of the Green Plants

The concepts and practices discussed above have been used to study the phylogeny of the green plants as a whole, as well as many smaller groups of taxa. Although the presence of chlorophylls *a* and *b* was long thought to be a unifying character (synapomorphy) for the green plants, the fascinating phenomenon of **endosymbiosis** has resulted in organisms that are not green plants yet still have chlorophylls *a* and *b*. Specifically, the euglenophytes and the chloroarachniophytes, groups once considered to be green algae, carry the remains (that is, the chloroplasts) of their green algal endosymbionts, yet are themselves in very different evolutionary lineages than green algae.

For the true green algae and land plants, the whole array of characters mentioned earlier (for example, morphology, biochemistry, anatomy, and molecular comparisons) have provided some clear understanding of the basic phylogeny for this all-important group—the green plants—upon which life depends.

One of the most interesting observations provided by current phylogenies is the fact that there are two major lineages of green photosynthetic organisms: the Chlorophyta, which includes only freshwater and marine green algae, and the Streptophyta, which includes some freshwater green algae and all of the land plants. Another interesting aspect of the phylogeny of

CHARACTER STATES

A botanist working with a particular group of flowering plants could observe that the flowers on some plants are red, whereas those on other plants are pink or white. The botanist might choose flower color as a character, with red, white, and pink as the character states.

If a character remains the same over generations with no changes, it will have only one state:

Pink—Pink—Pink—Pink—Pink

However, if the character changes in a species and the change is transmitted to descendants, there will be more than one character state:

Pink—White—White—White
\—Red—Red—Red

Choice of characters is one of the most important aspects of phylogenetic analysis. In the example above, flower color might be considered a good character if all species being examined have flowers of the same type, varying only in color. However, if the group contained species that did not ever flower, then the independence of the character flower color would be in question, because flower color would depend first on the presence or absence of flowers in general. Independence of characters is one of the main attractions of using molecular sequences for phylogenetic reconstruction. Since the early 1990s, use of sequence data from different genes has become so common in phylogenetic analysis that this methodology has its own term: molecular systematics.

endosymbiosis a symbiosis in which one organism lives inside the other.

CONVERGENT EVOLUTION

The evolution of similar features in organisms that do not share a recent common ancestor is termed convergence. Convergence is often the result of similar, selective environmental pressures acting on organisms in different parts of the world. The classic botanical example of convergent evolution involves three very different groups of flowering plants—cacti, spurges, and milkweeds—growing in similar desert environments in the New World, Asia, and Africa. The harsh desert environment favors adaptive characteristics that provide the capacity for water storage (such as large, fleshy stems) and protection from extremes of heat and dryness (reduced leaves or spines). Although members of these groups of plants resemble each other in appearance, they do not have a close common ancestor.

green plants is that there was a single origin of the land plants from a green algal ancestor. Botanists are not absolutely certain which of the algae living today are the most closely related to the land plants, but they have narrowed the field to two groups.

Phylogenetic studies have also robustly established that the bryophytes (the mosses, liverworts, and hornworts) are the most primitive land plants. But, interestingly, there is still some uncertainly about which type of bryophyte is most closely related to the green algae—the hornworts or liverworts.

For the green plants, the phylogenetic history is not completely resolved, and scientists will continue using various methods of phylogenetic investigation to constantly improve and refine the understanding of the exact evolutionary history of all green plants, that is, the true phylogeny. SEE ALSO Darwin, Charles; Endosymbiosis; Evolution of Plants; Systematics, Molecular; Systematics, Plant; Taxonomy.

Russell L. Chapman and Debra A. Waters

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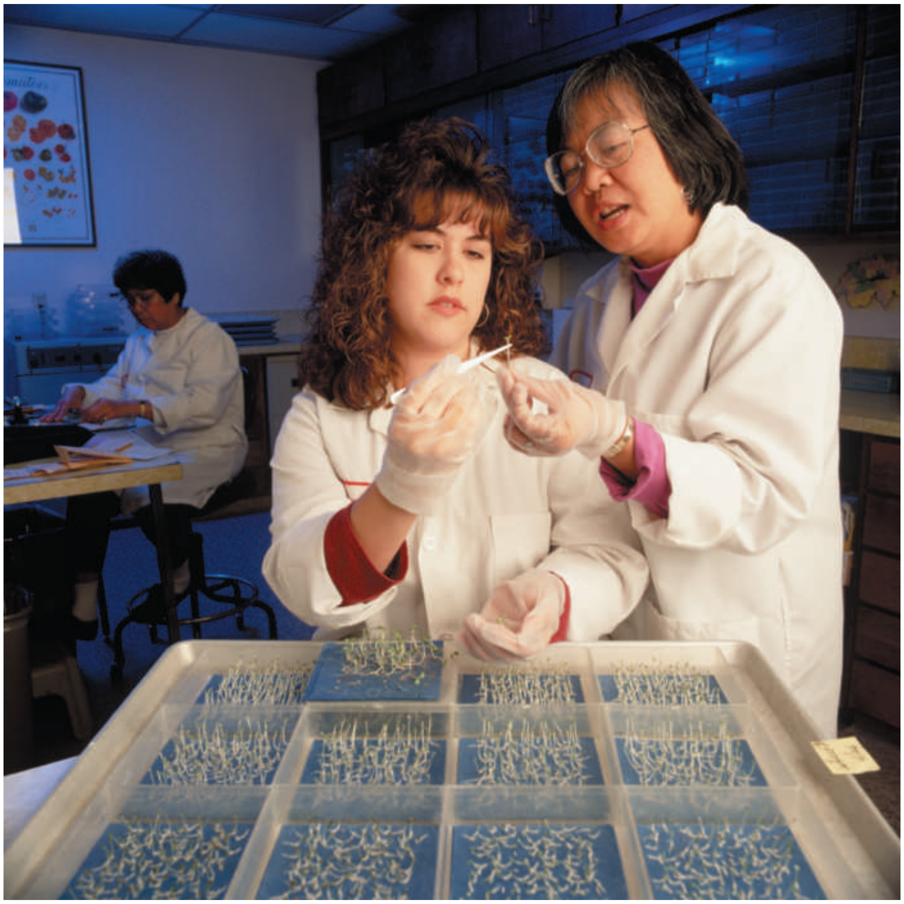
Physiologist

A plant physiologist studies a large variety of plant processes, such as how chemicals are transported throughout the plant, how plants capture the energy from the sun, and how plants defend themselves from attack by microbes or insects. Plant physiologists also study the process of plant growth and development: how plant cells perceive their place and role within the plant, how factors such as light and gravity affect what plant cells will do, and how plant hormones signal to cells about environmental conditions. Thus, plant physiologists may study the mechanisms by which plants produce **compounds** of medicinal value or the effect of increased carbon dioxide concentrations or drought stress on plant growth. Such research can lead to identification of medicines, may serve to determine how plants respond to the proposed greenhouse effect, and may be used to create plants resistant to drought stress. Overall the study of plant **physiology** can benefit humanity by providing an increase in crop yields for farmers or the identification of more effective medicines. A plant physiologist is responsible for designing, implementing, and interpreting experiments related to plant biology. Plant physiologists also serve as teachers of plant biology to students of all ages and may help inform politicians of the role of science in our daily lives.

compound a substance formed from two or more elements

physiology the biochemical processes carried out by an organism

In order to pursue a career in plant physiology an individual should obtain a bachelor's degree in plant biology or a bachelor's degree in biology



Researchers in a seed technology laboratory examining sprouts.

with an emphasis in plants. Further specialized study, such as obtaining a master's or doctorate in plant biology, are helpful in securing employment and ensuring career advancement. Laboratory training in the methods and rationale of plant physiology is essential.

Universities, industry, botanical gardens, government agencies, and conservation organizations employ plant physiologists. The work performed by plant physiologists can be pursued in a wide variety of environments. Some physiologists pursue research purely in the laboratory. They may cultivate their plant of interest in a greenhouse or growth chamber and use these plants to study a process of interest by performing experiments within the laboratory. Other plant physiologists study plants in their native environment and spend a great deal of time outdoors. Depending on what plant process is being studied these scientists may travel the globe, studying medicinal plants in the tropical rain forest or carbon fixation in the arctic tundra.

The career of a plant physiologist is exciting because it is forever changing. Each day experiments are performed that provide new insight into how plants function and allow for discoveries of the unknown. The work may give a person the satisfaction of having contributed to a knowledge base that will forever serve to improve the quality of life on this planet. SEE ALSO PHYSIOLOGY.

Sabine J. Rundle

Physiology

Plant physiology encompasses the entire range of chemical reactions carried out by plants. Like other living organisms, plants use deoxyribonucleic acid (DNA) to store genetic information and proteins to carry out cellular functions. **Enzymes** regulate both anabolism (buildup of complex **macromolecules**) and catabolism (the breaking down of macromolecules into simple molecules). Unlike animals, plants create a large variety of secondary metabolites, complex molecules with a range of specialized functions.

enzyme a protein that controls a reaction in a cell

macromolecule a large molecule, such as protein, fat, nucleic acid, or carbohydrate

Structure and Function of Macromolecules

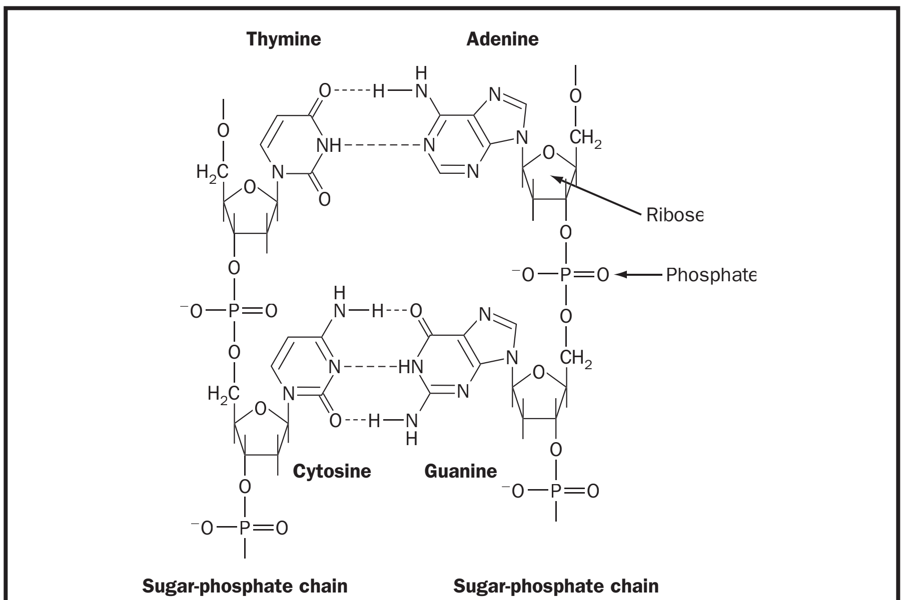
polymer a large molecule made from many similar parts

DNA. Deoxyribonucleic acid (DNA) is a high-molecular-weight **polymer**, containing phosphate, four nitrogen bases, and the pentose sugar deoxyribose. There are two pyrimidine bases, cytosine and thymine, and two purine bases, adenine and guanine. These nitrogen bases are joined to long chains of alternating sugar and phosphate. The three-dimensional structure of DNA consists of a two-stranded alpha-helix with each strand consisting of a long chain of polynucleotides and the strands joined through the bases by hydrogen bonding. The two strands are precisely complementary in their base sequence, since adenine in one chain is always paired with thymine on the other (and vice versa) and, similarly, guanine is always paired with cytosine (see the accompanying figure of the structure of DNA).

DNA occurs in the chromosomal material of the nucleus, closely associated with proteins called histones. In higher plants, DNA is also present in the **chloroplasts** and mitochrondria of each cell. The sequence of DNA codes for protein synthesis in such a way that different base triplets determine, in turn, the amino acid sequence of that protein.

chloroplast the photosynthetic organelle of plants and algae

RNA. Ribonucleic acid (RNA) is similar in structure to DNA except that a different sugar, ribose, is present and the thymine of DNA is replaced by uracil. RNA also differs from DNA in being single- rather than double-stranded and it is also more labile (unstable) than DNA. The purpose of



Basic structure of deoxyribonucleic acid (DNA).

RNA is to transfer the genetic information locked up in the DNA so that proteins are produced by the plant cell. In order to carry out this operation, there are three classes of RNA. Messenger RNA (mRNA) provides the exact template on which proteins of specific amino acid sequences are synthesized. Ribosomal RNA provides the site within the **cytosol** for protein formation. Transfer RNA (tRNA) makes up to 10 to 15 percent of the total cellular RNA, and serves an essential function in the decoding process of translating mRNA sequences into proteins. It carries amino acids to the ribosome, where they are linked together in the sequence dictated by mRNA. The result is a protein.

cytosol the fluid portion of a cell

Proteins. The proteins in plants, as in other organisms, are high-molecular-weight polymers of amino acids. These amino acids are arranged in a given linear order, and each protein has a specific amino acid sequence. In the simplest cases, a protein may consist of a single chain of amino acids, called a polypeptide. Several identical chains may, however, aggregate by hydrogen bonding to produce complex units with a much higher molecular weight. A polypeptide may coil up partly as an alpha-helix and thus adopt a particular three-dimensional structure. Many proteins are rounded in shape and hence are called globular proteins.

Many proteins are enzymes that catalyze particular steps in either primary or secondary metabolism. There are also many different storage proteins, found mainly in seeds, that provide a source of nitrogen in the young seedling. Perhaps the most important plant protein is ribulose 1,5-bisphosphate carboxylase, the essential catalyst for photosynthesis, which comprises up to 50 percent of the leaf protein in most green plants. Each green leaf, however, may synthesize up to one thousand different proteins, each with an assigned role in plant growth and development.

Polysaccharides. The chemistry of polysaccharides is, in a sense, simpler than that of the other plant macromolecules since these polymers contain only a few types of simple sugars in their structures.

The most familiar plant polysaccharides are cellulose and starch. Cellulose represents a very large percentage of the combined carbon in plants and is the most abundant organic **compound** on Earth. It is the fibrous material of the cell wall and is responsible, with lignin, for the structural rigidity of plants. Cellulose is known chemically as a beta-glucan and consists of long chains of $\beta 1 \rightarrow 4$ linked glucose units, the molecular weight varying from 100,000 to 200,000. Cellulose occurs in the plant cell as a crystalline lattice, in which long straight chains of polymer lie side by side linked by hydrogen bonding.

compound a substance formed from two or more elements

Starch differs from cellulose in having the linkage between the glucose units as $\alpha 1 \rightarrow 4$ and not $\beta 1 \rightarrow 4$ and also in having some branching in the chain. Starch, in fact, comprises two components, amylose and amylopectin. Amylose (approximately 20 percent of the total starch) contains about three hundred glucose units linked in a simple chain, which exists in vivo in the form of an alpha-helix. Amylopectin (approximately 80 percent) contains chains with regular branching of the main chain by secondary $\alpha 1 \rightarrow 6$ linkages. Its structure is thus randomly branched. Starch is the essential storage form of energy in the plant, and starch granules are frequently located within the chloroplast close to the site of photosynthesis.

The different classes of polysaccharide fall into two groups according to whether they are easily soluble in aqueous solutions or not. Those that are soluble include starch, inulin, pectin, and the various gums and mucilages. The gums that are exuded by plants, sometimes in response to injury or infection, are almost pure polysaccharide. Their function in the plant is not entirely certain, although it may be a protective one. The less-soluble polysaccharides usually comprise the structural cell wall material and occur in close association with lignin. Besides cellulose, there are various hemicelluloses in this fraction. The hemicelluloses have a variety of sugar components and fall into three main types: xylans, glucomannans, and arabinogalactans. They are structurally complex, and other polysaccharide types may also be found with them.

Anabolism and Catabolism: Biosynthesis and Turnover

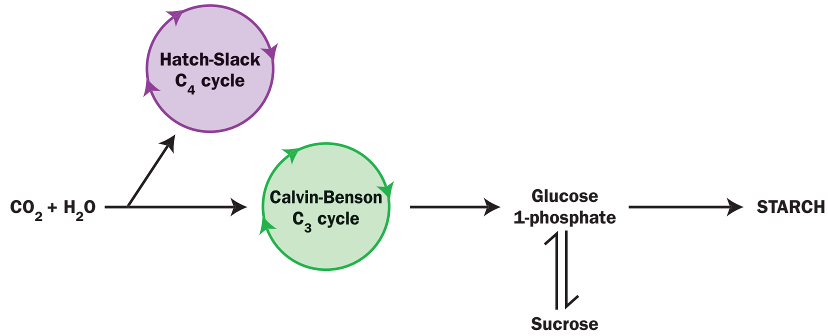
Anabolism. Anabolism is the energy-requiring part of metabolism in which simpler substances are used to build more complex ones. In plants, primary metabolites are built up from very basic starting materials, namely CO_2, H_2O, nitrate ($NO^{-}{}_{3}$), sulfate ($SO_4{}^{2-}$), phosphate ($PO_4{}^{3-}$), and several trace metals. Each metabolite is formed by a discrete biosynthetic pathway, each step in the pathway being catalyzed by a separate enzyme.

stomata openings between guard cells on the underside of leaves that allow gas exchange

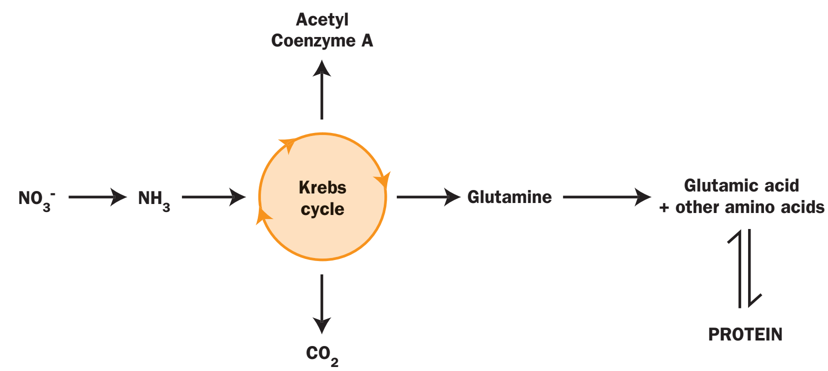
The most important anabolic pathway in green plants is the formation of starch from external CO_2 through the process of photosynthesis. Light energy is used to capture the atmospheric CO_2, taken in via the **stomata**, and convert it to sugar by condensing it with glycerophosphate, forming glucose 1-phosphate in the Calvin-Benson (C_3) cycle. In tropical plants, an additional carbon pathway is involved in photosynthesis, whereby the CO_2 is first captured by the plant in the form of simple organic acid such as malate. This is known as the Hatch-Slack (C_4) cycle, which provides a more efficient use of atmospheric CO_2. Regardless of the pathway, the glucose 1-phosphate is then used to produce starch. A similar end-product of carbohydrate metabolism is sucrose. Sucrose is important as an easily transportable form of energy within the plant. Starch, by contrast, is laid down mainly in the seed (e.g., of a cereal grain), and is not remobilized until that seed germinates in the following year.

Another equally important anabolic pathway in plants is that leading to protein synthesis. The starting material is usually inorganic nitrate taken in via the root from the soil and transported up the stem into the leaf. Here it is reduced to ammonia, which is immediately combined with alpha-ketoglutaric acid to yield glutamine. By a reshuffling process, glutamine is then converted to glutamic acid and by a variety of related processes the other eighteen protein amino acids are produced. These are then combined with tRNA and assembled together to yield the polypeptide chain(s) of protein.

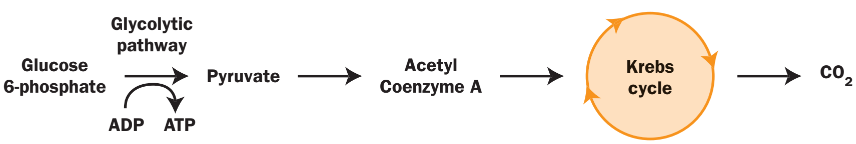
Yet another anabolic mechanism is the formation of a lipid (an oil or fat). Lipids are produced from fatty acids, formed in turn from acetyl-coenzyme A, a product of glycolysis. Lignin, the building strength in wood and in plant stems, is produced by a pathway starting from the sugar sedoheptulose, available from the Calvin-Benson cycle. The nucleic acids and their bases are formed from protein amino acids. Purines are produced from glycine while pyrimidines are produced from aspartic acid.



Anabolic pathway to starch via photosynthesis in chloroplast.



Anabolic pathway of nitrogen metabolism.



Catabolic pathway for oxiding photosynthetic sugar.

Catabolism. Catabolism includes any metabolic process involving the breakdown of complex substances into smaller products. Catabolism is thus the reverse of anabolism. No sooner is sugar available to the plant from photosynthesis than it is turned over and metabolized in order to provide the energy (e.g., in the form of adenosine triphosphate [**ATP**]) needed to drive the various processes that are taking place in the cell. Some ATP is provided in the process of glycolysis, by which glucose 1-phosphate is broken down to pyruvate and subsequently to acetyl-coenzyme A. The last stages in sugar metabolism include the entry of acetyl-coenzyme A into the Krebs tricarboxylic acid cycle. This process returns the carbon, originally taken in via photosynthesis, back into the atmosphere as respired CO_2, and each turn of the Krebs cycle provides more ATP for the cell.

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

A related pathway involving the Krebs cycle is the glyoxylate cycle, a pathway for lipid breakdown. This catabolic pathway can also become anabolic, converting the stored lipid into sugar.

In summary, every metabolite in the plant cell is subject to both anabolism and catabolism. In other words, there is a continual turnover, with the building up and breakdown of larger molecules. In general, anabolism involves the input of energy to build molecules, while catabolism involves the release of that energy when molecules are broken down. Thus, the plant is in a continual state of flux or metabolic activity throughout its life cycle.

Primary Metabolites vs. Secondary Metabolites

The compounds present in plants are conveniently divided into two major groups: primary and secondary metabolites. Primary metabolites are those produced by and involved in primary metabolic pathways such as respiration and photosynthesis. Secondary metabolites are clearly derived by **biosynthesis** from primary metabolites and are generally much more variable in their distribution patterns within the plant kingdom.

biosynthesis creation through biological pathways

Primary metabolites include the components of processes such as glycolysis, the Calvin-Benson cycle, and the Krebs cycle. Primary metabolites are virtually identical throughout the plant kingdom: they are mainly sugars, amino acids, and organic acids. As intermediates in metabolic pathways, these molecules may be present in some activated form. Glucose, for example, when taking part in metabolism, occurs in an energy-rich form as glucose 1-phosphate or as uridine diphosphoglucose. Other primary metabolites are the proteins, nucleic acids, and polysaccharides of plant cells. These have universal functions as enzymes, structural elements, storage forms of energy, and hereditary materials.

Secondary metabolites are produced by biosynthetic pathways, beginning with primary metabolites as starting materials. It has been estimated that about one hundred thousand secondary metabolites have been characterized in plants, and additional substances are continually being discovered. The amount of any secondary compound present in a plant is the result of an equilibrium between synthesis, storage, and metabolic turnover. Regulation of secondary metabolism is complex, and production may be limited to certain organs of the plant and may only take place during a single phase of the life cycle (e.g., during flowering or fruit formation).

Secondary metabolites are conveniently divided into three main chemical classes: the phenolics, the terpenoids, and the nitrogen-containing substances. The phenolics include the lignins, which are the aromatic materials of cell walls, and the anthocyanins, the colorful red to blue pigments of angiosperm flowers. Another phenolic class are the plant **tannins**, mainly present in woody plants, which have the special property of being able to bind to protein. They impart an astringent taste to plant tissues containing them and are significant flavor components in tea, wine, and other plant beverages.

tannins compounds produced by plants that usually serve protective functions; often colored and used for “tanning” and dyeing

The terpenoids are probably the most numerous of secondary substances. They are subdivided into monoterpenoids and sesquiterpenoids (essential oils); diterpenoids, including resin acids; triterpenoids (phytosterols, cardenolides, limonoids, etc.); and tetraterpenoids (**carotenoids**). The most visible terpenoids are the yellow to red carotenoid pigments present in flowers and fruits. Limonin gives lemon its characteristic taste. By contrast, volatile terpenoids give caraway and carrot their characteristic scents.

carotenoid a colored molecule made by plants

The nitrogen-based secondary metabolites are variously classified as amines, alkaloids, **cyanogenic** glycosides, and mustard oil glycosides. In general they have only limited occurrences. Alkaloids are the best known compounds of this type and are found in 20 percent of all plant families. Some alkaloids, such as morphine, because of their physiological activities in humans, have been used extensively in medicine. Other alkaloids, such as coniine from the hemlock, have been used as poisoning agents.

cyanogenic giving rise to cyanide

While the role of primary metabolites is clear, the functions of secondary substances are still uncertain. The anthocyanin and carotenoid pigments, together with the floral essential oils, are necessary to attract animals to flowers. The gibberellins, **auxins**, and cytokinins, together with abscisic acid and ethylene, control plant growth and development. Alkaloids and tannins deter animals from feeding on green tissues and thus are valuable to plants for limiting the extent of insect herbivory and animal grazing. SEE ALSO Alkaloids; Cacao; Carbohydrates; Carotenoids; Cellulose; Coca; Defenses, Chemical; Flavonoids; Lipids; Opium Poppy; Photosynthesis, Carbon Fixation and; Photosynthesis, Light Reactions and; Physiologist; Psychoactive Plants; Terpenes.

auxin a plant hormone

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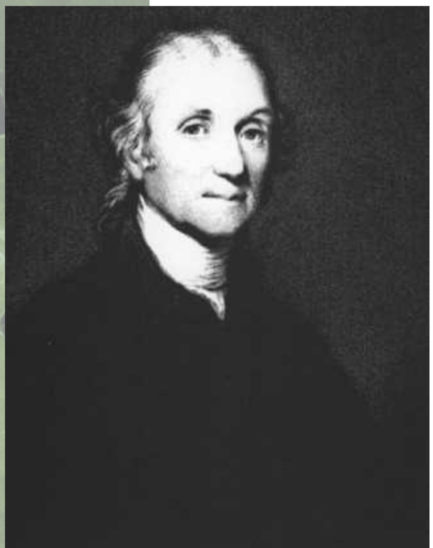
Physiology, History of

The history of physiology—the discipline concerned with the functioning of plants—can be organized around the discovery of several key processes.

One of the first physiological questions to be studied scientifically was how plants obtain food. Although we now know that plants manufacture carbohydrates from carbon dioxide and water via photosynthesis, the ancient Greeks reasoned that a plant's food must come from the soil. This idea persisted until the 1600s, when Jean Baptiste van Helmont performed an experiment in which he carefully weighed a pot of soil and planted a willow seedling in it. Over a period of five years he added nothing but water to the pot, and the willow grew into a tree weighing over one hundred pounds. When he cut down the tree he found that the soil weighed the same, less about two ounces, as when he began the experiment. Thus, the soil could not be the source of the plant's food. Van Helmont concluded it could have come only from the water he added.

The idea that air could be utilized by plants was first suggested by Stephen Hales in the early 1700s. Hales noticed bubbles exuding from the cut ends of stems and reasoned that air might enter the plant through its leaves and circulate to other organs. At that time air was considered a uniform substance, and it was not until the late 1700s that Joseph Priestley found that air in a closed container could be altered by a burning candle or a living an-



Joseph Priestley was the first to demonstrate that plants produce oxygen.

imal such that the flame would be extinguished and the animal would die. However, the presence of a plant in the container kept the candle burning and the animal alive. Priestley's results were the first to demonstrate that plants produce oxygen, now known to be a product of photosynthesis. Consequently, Jan Ingenhousz showed that oxygen is produced only by green parts of plants (and not roots, for example) and only in the light.

The remainder of the photosynthetic equation was elucidated largely by Nicholas de Saussure, who showed that during photosynthesis carbon dioxide is converted to organic matter, approximately equal amounts of carbon dioxide and oxygen are exchanged, and water is a reactant. In addition, Julius von Sachs, considered the founder of modern plant physiology, demonstrated that chlorophyll, located in **chloroplasts**, is involved. Thus, by the late 1800s photosynthesis could be summarized as follows:

chloroplast the photosynthetic organelle of plants and algae

$$6CO_2 + 6H_2O + \text{light}$$
$$\downarrow \text{ chlorophyll}$$
$$C_6H_{12}O_6 + 6O_2$$

In the 1930s C. B. van Neil suggested that the oxygen released in photosynthesis came from water rather than from carbon dioxide, and this was verified in the 1940s using **radioisotopes**. Details concerning the role of light were worked out by Robin Hill, Robert Emerson, and Daniel Arnon, and the reactions by which carbon dioxide is converted to carbohydrate were elucidated by Melvin Calvin and his colleagues in the early 1950s.

radioisotopes radioactive forms of an element

Mineral Nutrition and the Transport of Water, Minerals, and Sugars

It had long been known that water, along with dissolved minerals, enters a plant through its roots. Sachs demonstrated that plants do not require soil and can be grown in an entirely liquid medium as long as the medium contains the minerals required for survival. This technique of hydroponics facilitated studies of the mechanisms for mineral uptake by the roots.

Another contribution of Hales was to demonstrate how water is transported in the plant. Hales established that water passes upward from the roots to the leaves, where it is lost to the atmosphere by the process of **transpiration**. But it was not until 1895 that Henry Dixon and John Joly proposed the cohesion theory to explain how transpiration causes water and dissolved minerals to be pulled upward through the xylem.

transpiration movement of water from soil to atmosphere through a plant

The transport of carbohydrates was found to take place by a different mechanism. In the late 1600s Marcello Malpighi noticed that when the bark was removed in a ring around a tree the portion of the bark above the ring increased in thickness while the portion below the ring did not. Because ringed trees continue to transpire, the ringing process apparently did not hinder water transport but instead prevented the transport of other substances necessary for growth. Later it was shown that bark contains phloem tissue, which transports sugars from the leaves to other plant parts. The mechanism of sugar transport, termed translocation, was a mystery until 1926, when E. Münch proposed the pressure-flow model, in which the **osmotic** entry of water into the phloem generates a hydrostatic pressure that pushes the dissolved carbohydrates both upward to the shoot tip and downward to the roots.

osmotic related to the movement of water across a membrane, due to differerences in concentration of dissolved substances

Plant Hormones, Environmental Physiology, and Molecular Genetics

In the late 1800s Sachs suggested that the formation of roots and shoots was controlled by internal factors that moved through the plant. The first such factor, the plant hormone auxin, was discovered in 1928 by Fritz Went, building on experiments with phototropism by Charles and Francis Darwin, Peter Boysen-Jensen, and Arpad Paál. Went found that phototropism, the process by which stems bend toward the light, is the result of auxin migrating from the illuminated side of a **coleoptile** to the shaded side, where it stimulates growth. Over the next decades other plant hormones—most notably the gibberellins, cytokinins, ethylene, and abscisic acid—were discovered. Together with auxin, they regulate almost every aspect of plant growth and development.

coleoptile the growing tip of a monocot seedling

In the 1950s emphasis shifted to biochemical mechanisms underlying physiological and developmental processes. Particularly important was the discovery by Harry Borthwick and Sterling Hendricks in 1952 of phytochrome, a pigment involved in a variety of developmental responses including flowering, seed germination, and stem elongation. In addition, there was a trend toward environmental physiology, a discipline in which the methods of plant physiology are applied to the problems of ecology, including plant responses to extremes of cold, salt, or drought.

The 1970s introduced the era of molecular genetics. Plant physiologists use molecular genetics to localize and identify the genes on a chromosome, understand the mechanisms by which genes are expressed, and elucidate the processes involved in coordinating the expression of genes in response to environmental signals. SEE ALSO CALVIN, MELVIN; DARWIN, CHARLES; DE SAUSSURE, NICHOLAS; GENETIC MECHANISMS AND DEVELOPMENT; HALES, STEPHEN; HORMONES; HYDROPONICS; INGENHOUSZ, JAN; PHOTOSYNTHESIS, CARBON FIXATION AND; PHOTOSYNTHESIS, LIGHT REACTIONS AND; PHYSIOLOGIST; PHYSIOLOGY; PHYTOCHROME; SACHS, JULIUS VON; TRANSLOCATION; TROPISMS; VAN HELMONT, JAN BAPTISTE; VAN NIEL, C. B.; WATER MOVEMENT.

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Phytochrome

A plant grown in the dark appears long and spindly, is pale yellow, and has unexpanded leaves. When transferred to light, the growth rate of the stem slows, **chloroplasts** begin to develop and accumulate chlorophyll, and the primary leaves begin to expand and develop. Many of these dramatic changes are the result of activation of light receptors (photoreceptors) called phytochromes. Phytochromes are proteins with an attached pigment molecule that allows them to detect light, especially in the red

chloroplast the photosynthetic organelle of plants and algae

and far-red region of the spectrum. Depending on the light conditions, a phytochrome molecule may be converted to an active form or reconverted to an inactive form.

Most plants have more than one gene coding for different phytochromes, and these different products of the phytochrome gene family frequently control different responses to the light environment. Phytochromes regulate many aspects of plant growth and development by measuring the duration, intensity, and wavelengths of light. From the information gathered through phytochromes, a plant can determine the season, time of day, and whether it is growing beneath other plants versus in an open field. These photoreceptors control numerous functions throughout the life of the plant, including whether seeds germinate, how rapidly cells expand and divide, which genes are expressed, what shape and form a plant will take, and when the organism will flower and produce new seeds. SEE ALSO Photoperiodism; Rhythms in Plant Life.

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Pigments

Plant pigments are essential for photosynthesis, a process that supports all plant and animal life. They also play a key role in sensing light to regulate plant development and in establishing the communication between plants and the animals around them. Further, some plant pigments are the source of nutritional **compounds** required for or useful to the diets of humans and other animals.

compound a substance formed from two or more elements

The major classes of visible plant pigments are chlorophylls, carotenoids, flavonoids (including anthocyanins), and betalains. Each of these classes of pigments is composed of several individual compounds. For example, there are two major chlorophylls in higher plants, while there are hundreds of carotenoids and flavonoids that occur in nature. Phytochrome is a blue-green plant pigment that is not plentiful enough to be visible but serves as an important sensor of light, which stimulates plant growth and development.

Pigment Occurrence and Function

All plants contain chlorophylls and carotenoids in their leaves and other green plant parts. The chlorophylls are green and central to the process of photosynthesis. They capture light energy and convert it to chemical energy to be used not only by plants but by all animals.

The carotenoids and related xanthophylls are red, orange, or yellow and occur in green plant tissues along with chlorophylls in plastids, where they capture oxidizing compounds generated during photosynthesis. Without the protection they offer, photosynthesis cannot occur, so all photosynthetic tissue contains both the visible green chlorophylls as well as the masked orange carotenoids. Carotenoids serve another function as accessory light-harvesting pigments and photoreceptors that make photosynthesis more efficient.

Animals rely on plant carotenoids as their ultimate source of all vitamin A. Some of the carotenoids, including beta-carotene, possess a chemical structure that allows them to be converted to vitamin A by animals that consume them. Some animals also derive their pigmentation from carotenoids. For example, pink flamingoes and yellow goldfish obtain their colors from dietary carotenoids.

Anthocyanins and other flavonoids, betalains, and some carotenoids serve a key role in attracting the attention of animals for pollination, dissemination of fruit, seed, and storage organs, or warning of undesirable plant flavor or antinutritional compounds. These pigments provide visual cues to animals, alerting them to maturing plant organs without chlorophyll on the background sea of green leaves, stems, and immature flowers and fruit. Anthocyanins in red roses, grapes, and potatoes; betalains in beets; and carotenoids in daylilies, oranges, and carrots are some familiar examples.

The flavonoids include the red and blue anthocyanins that attract the human and higher-animal eye. Other flavonoids are the yellow and white flavonols, flavones, aurones, and chalcones. Some of these are brilliantly colored to insects, which can detect light absorbed in the near ultraviolet range. **Tannins** are complex flavonoids that contribute to the brown or black color of leaves, seeds, bark, and wood. The betalains are red and yellow pigments that occur in several families of higher plants and serve a function similar to that of anthocyanins. SEE ALSO Anthocyanins; Carotenoids; Chlorophyll; Flavonoids; Phytochrome.

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

Philipp W. Simon

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Plant Community Processes

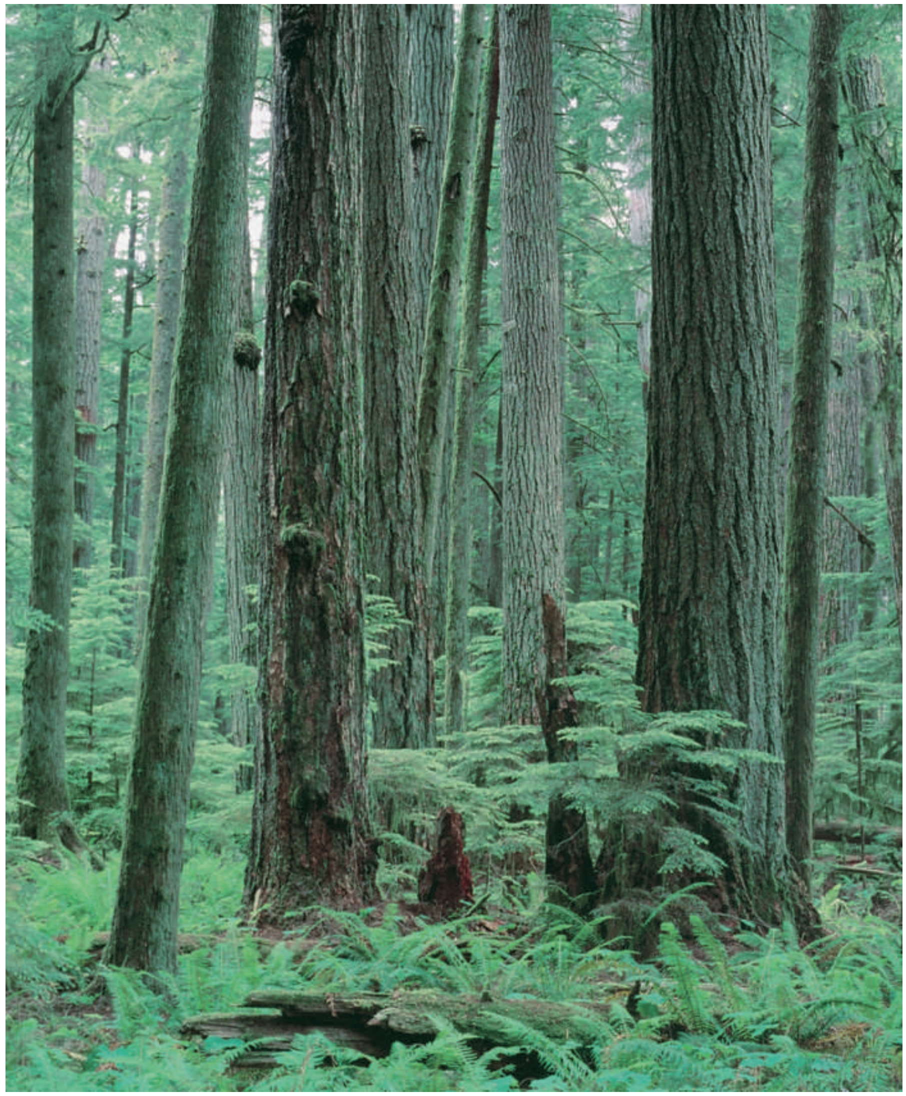
Ecosystems are formed from a mingling of nonliving **abiotic** components and the **biotic** community, which is composed of assemblages of living organisms. Many individuals in the biotic community are capable of capturing energy from sunlight through photosynthesis and, as a subset, form the plant community. The most prominent plants in the landscape are those with xylem and phloem forming **vascular** systems. While they are often the focus of plant community descriptions, green algae, mosses, and less-conspicuous plants also play a functional role in this ecosystem component. Heterotrophic organisms (including animals, bacteria, and fungi) feed on plants and form other subsets of the biotic community. These organisms are frequently examined along with plants in contemporary community studies. Understanding plant-plant, plant-animal, and animal-animal interactions has become a highly productive, community-level research area.

ecosystem an ecological community together with its environment

abiotic nonliving

biotic involving or related to life

vascular related to transport of nutrients



An old-growth Douglas-fir forest in the Pacific Northwest.

Community Concept

It is possible to use the term *plant community* in two different but intertwined ways. Frequently it refers to a description of what is growing at a specific location in the landscape, such as the plant community making up the woods behind your house or the vegetation in a marshy area beside a pond. These communities are real and you can walk out into them and touch the trees or pick the flowers. Foresters refer to these real communities as stands and the term can be extended to all types of vegetation. The other reference to a plant community is more abstract. The term can be used to describe the properties of a particular assemblage of plants that appears repeatedly in many different places. People living in the eastern United States immediately draw up a picture in their mind when the phrase "oak forest" is mentioned, while those in the Midwest and Southwest know what someone is referring to when the phrases "tall prairie grassland" or "hot desert" are used respectively. Ecologists expand this familiarity into lists of probable plants and predictable appearances such the shapes of the trees, leaf types, and height of the vegetation in various types of communities. They cannot predict exactly what will be in a stand at a specific location, but they can statistically describe what would most likely be found. These descriptions expand the understanding of the meaning of the abstract community so that scientists know what someone is describing, even if they have never been there themselves.

Community types are characteristically found in geographic locations with similar climate patterns and habitat characteristics. These large-scale segments of the terrestrial landscape are referred to as biomes. The description of the overall climatic conditions, appearance, and composition of the biomes is studied in the field of **biogeography**. Many different types of plant communities exist within each biome since there are many combinations of variation in the slope, moisture availability, soil type, exposure, elevation, and other habitat characteristics within these biogeographic regions.

biogeography the study of the reasons for the geographic distribution of organisms

Plant communities of different types form carpets of vegetation that cover smaller segments of geographic regions, such as the drainage basin of a river or the hillsides of a mountain. This patchwork of communities, and the corridors that connect them, is referred to as the landscape mosaic. This level of organization is intermediate in scale between the biome and individual communities. Landscape elements are not only interconnected spatially, but also by functional interactions. There are properties of the landscape, which emerge from these interdependencies, that cannot be predicted from community-level studies alone, as described by Richard Forman (1995).

Study of Communities

Plant ecologists over the years have developed many different techniques for gathering both descriptive and quantitative data from real stands, which can be used to characterize the abstract community types. *Terrestrial Plant Ecology* (1998), edited by Michael Barbour, includes an introduction to plant community sampling methodology and data analysis. John Kricher (1988 and 1993) uses a field guide approach to the understanding of the natural history of plant communities. Chapters covering community structure and function can be found in the references by Timothy Allen (1998), Manuel Molles (1999), and Robert Leo Smith and Thomas M. Smith (1998). The American roots of this discipline can be traced in *The Study of Plant Communities* (1956) by Henry J. Oosting, *Plant Communities: A Textbook of Plant Synecology* (1968) by Rexford Daubenmire, and *Plant Ecology* (1938) by John Weaver and Frederic E. Clements.

Plant community ecology can be traced back to the nineteenth century, when the Prussian biogeographer Fredrich Heinrich Alexander von Humbolt began to view vegetation as associations of plants and Johannes Eugenius Warming described various characteristics of different community types. Many other Europeans followed this line of research, notably Josias Braun-Blanquet, a central figure at the beginning of the twentieth century in what became known as the Zurich-Montpellier School of Phytosociology, where synecology (another name for community ecology) flourished.

Community Organization

The American ecologist Frederic Clements extended the community concept to the point where obligatory plant community composition and the resulting functional interactions were thought of as unique superorganisms, with individual species being as essential to their identity as the organs are to an animal. This idea prevailed from the 1920s until after the middle of the century, when Robert Whittaker carried out several studies in mountainous regions of the United States. He clearly demonstrated that a wide variety of intermediate community compositions existed in these complex environments and that those communities functioned perfectly well. What appeared to be a superorganism, with obligatory development patterns and species composition, just happened to exist over wide areas with similar habitat conditions. This was not a completely original idea. In 1926 Henry Gleason proposed that the appearance of obligatory groupings resulted from the success of individual species having similar environmental needs occurring together by chance. This was only shortly after the superorganism concept gained its foothold on scientific thought. However, until the evidence from Whittaker's methodical study was available to support Gleason's idea, many held that interactions between individuals produced community evolution similar to that proposed for species.

gradient difference in concentration between two places

The community is now seen as a many-dimensioned **gradient** of possible combinations of plant species. Readily identifiable community types exist because certain groupings that are successful under conditions occurring repeatedly in the landscape are more likely to be encountered than others.

Succession in Communities

One aspect of community organization accepted by ecologists is that the plants, animals, and microorganisms are very interconnected in function. Trees shade the forest floor and make it cooler than adjacent fields. Leaves from those trees decompose when they fall and provide nutrients for a variety of plants through their roots, which they may even reabsorb themselves. The same leaves could provide food for browsing animals while on the tree or for decomposing organisms as part of the litter on the forest floor. Fires, floods, volcanic eruptions, or human activities such as farming and forestry disrupt these interactions, but are not as disastrous to the long-term survival of the natural community as they might first appear, particularly if they do not occur with great frequency. This is because communities have self-repairing capabilities through the process of directional succession.

coppice growth growth of many stems from a single trunk or root, following removal of the main stem

If the disruption to the community is limited primarily to the biological matter above the ground and at least some of the soil remains intact, as is the case with an abandoned agricultural field, pasture, or recently burnt forest, the process is called secondary succession. This is a replacement process that is facilitated by a variety of mechanisms for the replacement of vegetation. In many cases, seeds are already present in the soil as part of a seed bank; sometimes wind or animals transport them in. Often, if the disruption has not been too severe, or if the regrowth is due to a change in land use, some vegetation, including weeds, will already be growing. It will become the basis for the early stages of successional development. In other cases, such as lumbering, where the tree trunks have been harvested, or where the aboveground parts were killed by certain types of fire, branches will sprout up from living roots. This produces what is called **coppice growth**, and one or more stems will produce a new tree trunk. Because of this process, the age of forest trees determined by counting rings in trunk wood may be a gross underestimate of the actual age of the organism as defined by the root tissue. Frequently more than one of these mechanisms will play a role in reestablishing plants in a disturbed area.

However, if there is no soil left at all, as is the case following a rockslide, the retreat of a glacier, or the development of vegetation on lava deposited from volcanic flows, then the process takes much longer. This is because at least some soil development is required before plants can become established in this process of primary succession. This sequential replacement on dry habitat sites is called xerarch succession, but can also occur when previously aquatic sites fill in through **sedimentation** resulting in the production of terrestrial communities called hydrarch succession. Changes under intermediate soil moisture conditions, including those for most secondary succession, occur in mesarch environments.

sedimentation deposit of mud, sand, shell, or other material

Different functional models exist to explain how succession proceeds. One model proposes that early species alter the environmental conditions and facilitate, or prepare the way, for species that occur in later stages. The second model suggests that some species become established early on in the process and inhibit the successful invasion by others. The third model does not involve facilitation or inhibition, but essentially holds that species that can tolerate the conditions that exist are successful in becoming established. Most likely all three processes can occur depending on conditions and timing.

Self-generating or autogenic succession leads to changes in community structure and ecosystem function. In the late 1960s, Eugene Odum described this as an overall strategy for ecosystem development. Even though general patterns of change appear to emerge, exceptions sometimes occur. There are, however, tendencies toward increases in **biodiversity** as succession progresses with slight declines as systems mature. Similarly, complexity and structure increase as succession proceeds, and increased proportional amounts of energy flow are needed to support increasing living community **biomass**; there can be a tightening of nutrient cycling as the systems age. Thirty years later, Odum (1997) updated his thoughts in light of extensive research stimulated by the original model. In addition to **systemic** changes such as these, there are also plant life cycle strategies such as high seed number production, aggressive seed dispersal, high sunlight preferences, and rapid growth amongst invasive species that appear early in succession. These are in contrast with the shade-tolerant, slower-growing, longer-lived species that play a larger role as the system matures. Fundamentally, as succession progresses, the organisms change the environment and in turn, the environment alters the relative success of individuals within the communities.

biodiversity degree of variety of life

biomass the total dry weight of an organism or group of organisms

systemic spread throughout the plant

Competition Within Communities

Because plant communities are composed of organisms with similar overall climatic requirements, and because resources such as nutrients, light, and water are present in finite amounts, there is a continuing interaction between individuals that determines their success in capturing and utilizing these resources. This interaction takes various forms and is referred to as competition. Competition is one of several different types of individual

predation the act of preying upon; consuming for food

mutualism a symbiosis between two organisms in which both benefit

obligate required, without another option

interactions that plants can be involved in and includes forms of exploitation, such as seed **predation**, herbivory, and parasitism; cooperation, such as **mutualism,** which may or may not be obligatory; and other specialized relationships. When the individuals are of the same type, the competition is said to be intraspecific, and when they are different, the interaction is interspecific. The term symbiosis is used to describe interspecific interactions involving close and continual physical contact and may be either deleterious, as in parasitism, or highly beneficial, as in the case of **obligate** mutualism.

Competition is somewhat unique in comparison to most other relationships, where at least one of the interacting individuals benefits from the interaction when it occurs. When competition is occurring, both partners to the interaction are most likely adversely affected. The most intense competition occurs between individuals with very similar needs. Consequently, intraspecific competition generally has a greater impact on the success of a particular plant in the community than interspecific competition. However, if most individuals of one species are more successful than most of another, then there will be more of them present. Since they lack the social organization of animals, complex coordinated group competition is unlikely to be an important aspect of competition in plants; in the case of plant competition, the interaction between individuals is more likely to be significant.

Competitive Exclusion and the Ecological Niche

The result of the interaction can affect the relative success of populations of a species and ultimately the community composition. In the 1930s, the Russian microbiologist G. F. Gause performed laboratory experiments that led to the conclusion that when populations of two different species are directly competing for a common resource in a limited environment, only one will ultimately be sustained in that space. The other will die out. This idea has come to be known as Gause's competitive exclusion principle. If this principle were to be valid in natural environments, then the number of surviving species would be greatly limited. However, this is not the case, particularly in complex plant communities.

The solution to this perplexing puzzle has been found in a process known as resource partitioning. Even some very obvious situations—where resource demand overlap between individuals clearly exists—demonstrate subtle differences in the way that the resource is exploited when examined in detail. Roots of one individual or species may penetrate to slightly different depths in the soil from another, or flowering times might be a few days different, thereby reducing competition for the services of a particular pollinator.

The entire complex of resource, habitat, physical, and other requirements that define the role of an organism within its community is called its ecological niche. The more similar the niches of two individuals or species, the greater the niche overlap. The greater the niche overlap, the greater the competition. The species composition of a community is a result of the way that individuals of different species with different niches can be packed together. Increases in the number of species within a community are accomplished by specialization, the reduction of the sizes of the niches, and efficient packing to reduce overlap. The number of niches that exist in a community is directly related to species diversity, the number of different types of organisms that can be supported.

Competitive Interactions

The plant community is a dynamic, competitive environment. Community composition exists in steady state, a status of apparent equilibrium, for varying periods of time. A pulse disturbance such as a fire, or more chronic stresses such as disease, evolutionary change, or global warming may alter the status quo. Increased global mobility of plant seeds and fragments of tissue, as well as various pathogens and disease vectors such as insects, have increased the chances of incursion by invasive species or the introduction of new competitors, which may lead to significant alterations in community composition. Because of this flexibility and inherent resilience, communities persist over time, even though the presence of specific organisms varies.

The intense defense of resources and the aggressive forays to acquire the essentials for survival by plants are not necessarily obvious. Competition between animals can be physical combat, and plants analogously can physically grow into the space occupied by another individual and crowd it out. However, the adaptations that make plants successful as competitors are generally more indirect. Examples of this include plants with more vigorous canopy growth that intercept the available light, or the individual with the healthier and more extensive root system that is more efficient at obtaining nutrients from the soil. Sometimes, just being able to grow faster is sufficient to give a competitive advantage. Many species have evolved to produce **toxins** that inhibit the growth of other plants, a condition known as allelopathy, and this can give them a competitive edge, particularly in the case of interspecific competition where self-inhibition is limited. SEE ALSO Allelopathy; Biogeography; Biome; Clements, Frederic; Interactions, Plant-Plant; Odum, Eugene; Symbiosis.

toxin a poisonous substance

W. Dean Cocking

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Plant Prospecting

Plant prospecting is the seeking out of plants for the development of new foods, prescription drugs, herbal dietary supplements, flavors and fragrances, cosmetics, industrial materials, pesticides, and other profitable products. Plant prospecting includes the selection and collection of plants from terrestrial, marine, and other aquatic **ecosystems** by expeditions to diverse areas of the world, such as tropical and temperate rain forests as well as arid and semiarid lands in Latin America, Africa, Australia, and Asia.

ecosystem an ecological community together with its environment

Field studies involve collecting plant samples in the wild for identification and labeling the samples for voucher, or reference, **specimens**. The specimens are deposited in herbaria, which are collections of preserved plants. If searching for plants for drug discovery programs, one kilogram of each plant species is typically gathered for further work in the laboratory. A plant extract is produced for screening for biological activity, followed by chemical isolation and identification of the compounds responsible for activity.

specimen object or organism under consideration

Botanists follow either random or targeted approaches when choosing plants for pharmacological studies and drug discovery. The random prospecting strategy is to gather all of the available vegetation in an area supporting rich biological diversity. The more focused methods are taxonomic, ecological, and ethnobotanical. The taxonomic method emphasizes the collection of close relatives of plants already known to produce useful compounds for medicine or other uses. The ecological approach focuses on plants that offer certain clues promissory of activity, such as plants free from herbivore predation, which imply the presence of chemical defenses. Finally, ethnobotanical prospecting is done by interviewing native healers who have knowledge of the local plant's medicinal properties.

The value of plant prospecting to the pharmaceutical industry is enormous. Some extremely effective treatments in modern medicine are derived from flowering plants in nature. Many prescription drugs contain molecules derived from, or modeled after, naturally occurring molecules in **vascular** plants. Tropical rain forests, with one-half or 125,000 of the world's flow-

vascular related to transport of nutrients

A biologist collects plant specimens from the forest floor in Poland's Bialowieza National Park.

ering plant species, are the source of forty-seven commercial drugs, including vincristine (Oncovin), vinblastine (Velban), codeine, curare, quinine, and pilocarpine. Vincristine is the drug of choice for the treatment of childhood leukemia; vinblastine is used for the treatment of Hodgkin's disease and other neoplasms.

The potential value of the existence of undiscovered plants for use as drugs for modern medicine and other plant products of economic interest provide an incentive to conserve species-rich ecosystems throughout the world. A fear shared by many is that plant species, as well as tribal healing and conservation knowledge, will vanish before they are studied and recorded.

Because developing countries are rich in plant **biodiversity** but technology-poor, while developed countries are biodiversity-poor but technology-rich, arrangements should be made to compensate the holders of plant resources when these are used to make patentable and economic products. Efforts are underway to establish property rights of plant biodiversity, as yet-undiscovered drugs will become another powerful financial incentive to conserve tropical forests and other ecosystems. The 1992 Convention on Biological Diversity established for the first time international protocols for protecting and sharing national plant and other biological resources and specifically addressed issues of traditional knowledge. SEE ALSO HERBARIA.

Barbara N. Timmermann

biodiversity degree of variety of life

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Plants

Plants are photosynthetic multicellular eukaryotes, well-separated evolutionarily from photosynthetic **prokaryotes** such as the **cyanobacteria**. Three **lineages** of photosynthetic eukaryotes are recognized: 1) green plants and green algae, with chlorophylls *a* and *b* and with **carotenoids**, including beta-carotene, as accessory **pigments**; 2) red algae, having chlorophylls *a* and *d*, with phycobilins as accessory pigments; and 3) brown algae, golden algae, and **diatoms**, with chlorophylls *a* and *c* and accessory pigments that include fucoxanthin.

Plants are differentiated from algae based on their exclusive multicellularity and their adaption to life on land. However, these two groups are so closely related that defining their differences is often harder than identifying their similarities. Fungi, often considered to be plantlike and historically classified with plants, are not close relatives of plants; rather, they appear to be closely related to animals, based on numerous molecular and biochemical features. Fossil evidence indicates that plants first invaded the land approximately 450 million years ago. The major groups of living land plants

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

lineage ancestry; the line of evolutionary descent of an organism

carotenoid a colored molecule made by plants

pigments colored molecules

diatoms hard-shelled single-celled marine organisms; a type of protist are liverworts, hornworts, and mosses (collectively termed bryophytes); lycophytes, ferns, and horsetails (collectively pteridophytes); and five lineages of seed plants: cycads, *Ginkgo*, gnetophytes, conifers (gymnosperms), and flowering plants (angiosperms). SEE ALSO ALGAE; ANATOMY OF PLANTS; ANGIOSPERMS; BRYOPHYTES; ENDOSYMBIOSIS; FUNGI; GYMNOSPERMS; PIGMENTS.

Doug Soltis and Pam Soltis

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Plastids

mitochondria cell organelles that produce ATP to power cell reactions

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Use for storage and maintaining internal pressure

endoplasmic reticulum membrane network inside a cell

compound a substance formed from two or more elements

micron one millionth of a meter; also called micrometer

genome the genetic material of an organism

chloroplast the photosynthetic organelle of plants and algae

meristematic related to cell division at the tip

All eukaroytic cells are divided into separate compartments, each surrounded by an independent membrane system. These compartments are called organelles, and they include the nucleus, **mitochondria**, **vacuoles**, Golgi bodies, **endoplasmic reticulum**, and microbodies. In addition to these organelles, plant cells contain a compartment that is unique to them. This is the plastid.

General Description of Plastids

Plastid is a term applied to an organelle that is exclusive to plant cells. Most of the **compounds** important to a plant, and to human diet, start out in the plastid. It is the place in the cell where carbohydrates, fats, and amino acids are made. As the name suggests, the plastid is plastic (i.e., changeable) in both appearance and function, and the different types of plastids can change from one type to another. The signals that trigger these changes can come from within the plant itself (e.g., developmental changes such as fruit ripening or leaf senescence) or from the surrounding environment (e.g., changes in day length or light quality). Despite this plasticity, all plastids have the following features in common: They are 5 to 10 **microns** in diameter and approximately 3 microns thick, are all surrounded by a double membrane termed the envelope that encloses a water-soluble phase, the stroma, and they all contain deoxyribonucleic acid (DNA) and ribonucleic acid (RNA).

The presence of DNA is one indication that plastids used to exist as free-living organisms. Plastids would have once contained all of the genes necessary for their growth and development. Although plastid DNA (the plastid **genome**) still encodes many essential plastid components, most of the genetic information now resides in the nucleus. During evolution most of the DNA became integrated into the nucleus so that the host cell controlled the genes needed for division and development of plastids. This important evolutionary step has consequently enabled the host cell to control most features of plastid structure and function. Thus, distinct types of plastids are found in different cells and tissues of the plant.

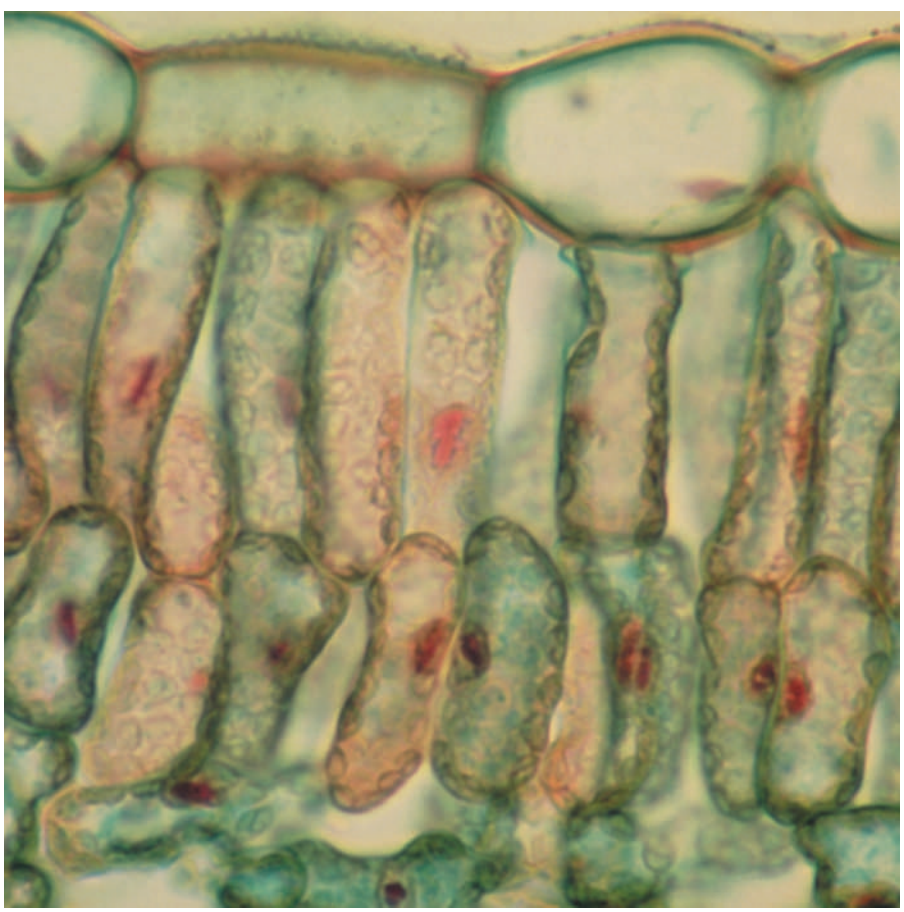
Eoplasts

Eoplasts (*eo*, meaning "early") represent the first stage of plastid development. They are spherical and lack any obvious internal membranes of the kind seen in **chloroplasts**. They occur in young, dividing cells of a plant (i.e., the **meristematic** cells) and are functionally immature. Their presence in egg cells prior to pollination means that they are transferred through generations via maternal inheritance. This means that eoplasts can only be made from preexisting eoplasts inherited via the egg. Eoplasts are able to divide along with the cell so that their number is maintained during plant growth. Increases in eoplast numbers occur when they continue to divide after cell division is complete. This is accompanied by cell differentiation, where the cell becomes specialized, and the eoplast matures into one of the functional types of plastid described next.

Chloroplasts

Chloroplasts are plastids found in photosynthetic tissue. This includes leaves, but also green stems, tendrils, and even fruit. Unripe tomato fruit, for example, contains chloroplasts as long as the tissue is green. On ripening, the chloroplasts change into chromoplasts and accumulate the pigments responsible for the red coloration of ripe fruit. Chloroplasts are distinguished from all other types of plastids by the presence of a complex organization of the internal membranes that form thylakoids. These form stacks of parallel membranes (called granal stacks) that contain the light-harvesting complexes involved in capturing light energy for use in photosynthesis. The chloroplast is the location of the photosynthetic processes occurring within the tissue. As well as the light-harvesting reactions, the **enzymes** responsible for carrying out the fixation of carbon dioxide, in a process called the Calvin-Benson cycle, are also located here. A mature cell of a cereal leaf, such as wheat, can contain up to two hundred chloroplasts.

enzyme a protein that controls a reaction in a cell



A cross-section micrograph of chloroplasts in a lilac leaf.

Chloroplasts are formed from the eoplasts present in very young leaf cells. Another route, although less common in nature, is for them to form from etioplasts, but this happens only if the leaves have been kept out of the light for several days and then transferred back into sunlight.

Etioplasts

Etioplasts are a special type of plastid that only occurs in leaf tissue that has been kept in the dark for several days. This dark treatment causes the leaves to lose their green color, becoming pale yellow and losing their ability to photosynthesize. These leaves are described as being etiolated, hence the term etioplast. Etioplasts are characterized by containing semicrystalline structures called prolamellar bodies made up of complex arrays of membranes. When etiolated leaves are exposed to the light, the leaves turn green and the etioplasts change into chloroplasts within a very short time. The membranes of the prolamellar body are converted into the thylakoid membranes, and chlorophyll is formed together with all of the enzymes needed for photosynthesis. All of these processes are reversible. When green leaves are put back into continued darkness for several days, the chloroplasts revert once more to etioplasts.

Chromoplasts

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

Chromoplasts (Greek *chromo*, meaning "color") are colored plastids found in flower petals and **sepals**, fruit, and in some roots, such as carrots. They are colored because they contain pigments. These are the carotenoids, and they produce a range of coloration including yellow, orange, and red. The purpose of this coloration is to attract pollinators and, in the case of edible fruits, animals that will aid fruit and seed dispersal. Sometimes the color may act as a warning signal to tell insects and animals that the plant is poisonous. As noted above, chromoplasts may be formed from chloroplasts as green fruit ripens and matures. Alternatively, they may be formed from the conversion of amyloplasts or by development of eoplasts.

Leucoplasts

Leucoplasts are colorless, nonphotosynthetic plastids found in nongreen plant tissue such as roots, seeds, and storage organs (e.g., potato tubers). Their main function is to store energy-rich compounds, and types of leucoplasts include amyloplasts and elaioplasts. Amyloplasts store starch and elaioplasts contain oils and fats. In roots, amyloplasts serve two important functions. Their high starch content makes them relatively dense, and this is thought to be important in helping the root to respond to gravity (geotropism). Root amyloplasts are also very important in that they contain many of the enzymes needed for converting inorganic nitrogen taken up from the soil (as nitrate and ammonium) into organic forms, such as amino acids and proteins. Starch is a major food product and as a consequence, a lot of current research is aimed at understanding how amyloplasts work and what controls the rate of starch formation in these plastids. Similarly, the formation of oils (e.g., in oil seed rape seeds) in elaioplasts is being studied in many research and industrial laboratories throughout the world. SEE ALSO Cells; Chloroplasts; Endosymbiosis.

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Poaceae *See Grasses.*

Poison Ivy

Poison ivy (*Toxicodendron radicans*) is a nuisance plant that grows throughout the continental United States. It grows in almost any type of soil, in both the shade and the sun. While it is most commonly found as a trailing vine, it can also form an upright shrub, and can climb trees, boulders, or walls to heights of 15 meters (50 feet). Its seeds are an important winter food for many types of birds.

Poison ivy's oil causes an itchy, blistering rash in most people who come in contact with it. All parts of the plant contain the oil, although the leaves are the most easily bruised and are therefore the most likely to cause the rash. The oil is sticky and will cling to (and be spread on) skin, clothing, tools, and animal fur. It is also spread in smoke when the plant is burned. In fact, irritation from poison ivy smoke is a major cause of temporary disability in forest fire fighters.

The active ingredient of the oil is urushiol (you-ROOSH-ee-ol). Urushiol is absorbed quickly into the skin. The itching and blistering that results is not due to direct damage done by urushiol, but by the allergic reaction mounted by the immune system. Relatively few people are actually immune to the effects of urushiol, although sensitivity varies and can change over time. Washing the oil off immediately after contact can help reduce the likelihood of developing a rash. In recent years, a clay-based lotion has been shown to help prevent the rash by binding to the urushiol before it can penetrate the skin.

Rashes last approximately two weeks. Some people find relief from the itching and blistering by applying calamine lotion or the mucilaginous sap of jewelweed (*Impatiens capensis*). Hot water can provoke a short-lived, in-

Poison ivy.

tense irritation followed by a longer period of relief. Prescription corticosteroid creams are used for severe cases.

Recognizing the plant is the best way to avoid it. The three leaflets of poison ivy are from 3 to 15 centimeters long, smooth to slightly indented at the edges, shiny and reddish in spring but becoming a glossy to dull green in summer. "Leaflets three, let it be; berries white, poisonous sight" is a handy way to remember the characteristic appearance of poison ivy.

Poison oak, which grows in California, Oregon, and Washington, has a somewhat similar appearance, while poison sumac grows as a shrub and has a compound leaf and drooping clusters of green berries (unlike other sumacs, which have upright clusters or red berries). All three plants are members of the family Anacardiaceae, many of whose members—including mango and cashew—also contain skin irritants in some plant parts. SEE ALSO Defenses, Chemical; Lipids; Poisonous Plants.

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Poisonous Plants

A plant or mushroom is considered poisonous or toxic if the whole organism, or any part of it, contains potentially harmful substances in high enough concentrations to cause illness or irritation if touched or swallowed. From the waxen-leaved dieffenbachia in your living room to the delicate foxglove blooming in your garden to the shoots sprouting from a forgotten potato in your refrigerator, poisonous plants are a common part of our lives. Since it is neither desirable nor practical to eliminate poisonous plants from our surroundings, we need instead to educate ourselves about their potential dangers. At the same time we need to understand that, like all plants, poisonous species have important ecological roles and many of them are also useful to us as medicines or for other purposes.

Some plants and mushrooms are extremely toxic and can quickly cause coma or death if consumed. Others, though slower acting, can also cause severe reactions. In the event of suspected poisoning by a plant or mushroom, it is imperative to seek medical attention immediately. There are poison control centers affiliated with hospitals and clinics throughout North America, where specialists can help and advise in cases of poisoning. Correct identification of the poison is essential for proper treatment. If you are seeking medical help for suspected poisoning and you do not know the plant or mushroom involved, be sure to bring along a sample, raw or cooked, for verification. Children and pets are especially vulnerable to accidental poisoning by plants and mushrooms. Of the hundreds of cases of such poisoning reported each year, however, only a very few actually result in serious illness or death.

Why Are Plants Poisonous?

Producing toxic chemical substances is often beneficial to plants, making them less palatable and providing them with protection against plant-eating animals or insects. Milkweeds, for example, produce several types of

A baneberry bush, a perennial herb of the buttercup family (genus *Actaea*) with poisonous berries.

toxins that render them generally distasteful to foraging animals. A mere taste of the bitter leaves will turn away most would-be browsers, unless they are extremely hungry.

toxin a poisonous substance

compound a substance formed from two or more elements

Many toxic **compounds** are secondary metabolites, which are produced as by-products of a plant's primary physiological processes. In some cases scientists do not yet understand why a particular type of plant or mushroom produces such poisons. Even within a single species, some individuals may have high concentrations of toxic compounds while others have minimal amounts. Over thousands of years, in the process of **domesticating** plants, we have learned to select and **propagate** less-toxic strains, and by these means, humans have been able to convert poisonous species into major foods. The common potato (*Solanum tuberosum*) is a good example; its wild relatives in the South American Andes are bitter and toxic due to intense concentrations of harmful **alkaloids**. Indigenous horticulturalists over many generations developed sweet and edible varieties of potato and learned how to process them to minimize these toxins. The Spanish introduced potatoes to the rest of Europe some time in the late 1500s, and, after a period of doubt and suspicion, they were adopted as a staple in many countries. Still, the domesticated potato produces harmful alkaloids in its leaves, fruits, and sprouts, and even in its tubers if they are left exposed to light and start to turn green. Many relatives of the potato, including **belladonna** (*Atropa belladonna*), black nightshade (*Solanum nigrum*), henbane (*Hyoscyamus niger*), and tobacco (*Nicotiana* spp.), contain these alkaloids and are thus quite poisonous to humans and animals.

domesticate to tame an organism to live with and to be of use to humans

propagate to create more of through sexual or asexual reproduction

alkaloid bitter secondary plant compound, often used for defense

belladonna the source of atropine; means "beautiful woman," and is so named because dilated pupils were thought to enhance a woman's beauty

Important Poisonous Compounds Found in Plants and Mushrooms

Alkaloids. There are many different kinds of plant and mushroom toxins. Alkaloids, the major type of poisonous compound found in the potato and its relatives, are common and widely distributed in the plant kingdom, especially but not exclusively among the flowering plants or angiosperms. Alkaloids are compounds derived from amino acids and are alkaline in nature.

Their molecular structure is cyclical, and they all contain nitrogen. They are generally bitter tasting, and many are similar in chemical structure to substances produced by humans and other animals to transmit nerve impulses. Consequently, when ingested, they often affect animals' nervous systems. Many alkaloids, while potentially toxic, are also valued as medicines. Some, like the caffeine found in coffee (*Coffea arabica*), tea (*Camellia sinensis*), and other beverages, are consumed by humans all over the world as stimulants. One particularly useful alkaloid-containing plant is ipecac (*Cephaelis ipecacuanha*), a plant in the coffee family. Syrup of Ipecac, made from this plant, causes vomiting when swallowed, and this makes it one of the most useful treatments for poisoning or suspected poisoning by plants or mushrooms. It is a standard item in poison control kits, but should never be used without medical advice.

Glycosides. Glycosides are another type of toxic compound, even more widely distributed in plants than alkaloids. These highly variable compounds consist of one or more sugar molecules combined with a non-sugar, or aglycone, component. It is the aglycone that usually determines the level of toxicity of the glycoside. For example, one class of glycosides, the **cyanogenic** glycosides, break down to produce cyanides, which in concentrated doses are violently poisonous. Cyanogenic glycosides are found in many plants, including the seed kernels of cherries, apples, plums, and apricots. They can be detected by the bitter almond smell they produce when the tissues are broken or crushed. In small amounts they are not harmful, but swallowing a cup of blended apricot pits could be fatal.

cyanogenic giving rise to cyanide

Like alkaloids, many glycosides have important medicinal properties. Foxglove (*Digitalis purpurea*), for example, produces digitalis and related compounds. These are cardioactive glycosides affecting the functioning of the heart. Foxglove has been used with great care as an herbal remedy by knowledgeable practitioners for centuries. In Western medicine, digitalis and its chemical relatives digoxin and digitoxin have wide application as drugs to help regulate heart function and treat heart-related illnesses. The same glycosides in foxglove that make it a useful medicine, however, can be deadly in the wrong dosage.

Oxalates. Other types of toxic substances include oxalates, which can interfere with calcium uptake. Calcium oxalate crystals are found in plants of the arum family, like skunk cabbage (*Lysichitum* spp., *Symplocarpus* spp.), rhubarb (*Rheum raponticum*), philodendron, and dieffenbachia. If ingested, these minute crystals cause intense burning and irritation to the tissues of the tongue and throat. The name dumbcane is sometimes used for dieffenbachia because it can make a person unable to speak by causing swelling of the tongue.

Many other classes of compounds, including **tannins**, alcohols, resins, volatile oils, and even proteins and their derivatives, can be toxic to humans and animals. Some types of toxins, phototoxins, are activated by ultraviolet light and can cause intense irritation to the skin but only if the affected area is exposed to ultraviolet light, such as in sunlight.

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

Perhaps the most insidious plant substances are those that are cancer-causing (carcinogenic), because their effects are more long-term and not easily traced. Some fungi, especially certain molds, such as *Aspergillus flavus*, which grows on improperly stored peanuts, are known to produce tumor-inducing substances; *Aspergillus* produces carcinogens called aflatoxins that can cause liver cancer.

Some toxins are so concentrated that only the tiniest amount can be fatal. The seeds of castor bean (*Ricinus communis*), for example, produce a high molecular weight protein called ricin, which is reputed to be one of the most toxic naturally occurring substances known. Ricin inhibits protein synthesis in the intestinal wall. It and other proteins of its type, called lectins, are violently toxic; eating one to three castor bean seeds can be fatal for a child, two to six for an adult. (Ricin injected from an umbrella tip was used to assassinate the Bulgarian dissident Georgi Markov while he waited for a bus in London in 1978.)

Plants Poisonous to Livestock

Plant species that are poisonous to humans are also commonly poisonous to other animals. Still, it is dangerous to assume that a plant that does not harm another animal will also be edible for people. Some rabbits, for example, are known to eat belladonna, which can cause abdominal pain, vomiting, fever, hallucinations, convulsions, coma, and even death when eaten by humans. These rabbits possess an **enzyme** that allows them to break down the toxic alkaloids of belladonna into digestible ones. Also, many ruminants or range animals with multiple stomachs like cattle, sheep, and goats, have a higher capacity for ingesting toxic plants without being harmed than animals with single-stomach digestive systems, such as humans, pigs, and horses.

enzyme a protein that controls a reaction in a cell

Livestock poisoning causes many problems and economic losses for farmers and ranchers. Usually, animals will avoid toxic plants because of their bitter, unpleasant taste. If the range is poor, however, or in winter and early spring when forage is scarce, livestock may begin feeding on poisonous plant species, and even develop a taste for them, leading to repeated poisonings or death. Malformed or stillborn young can also result from pregnant cows, mares, or ewes eating poisonous species. A usually fatal type of birth deformity in lambs, called monkeyface, was traced to ewes feeding on an alkaloid-containing plant of the lily family, false hellebore (*Veratrum californicum*), in their early pregnancy. Ensuring that pastures are not overgrazed and that animals have a good source of food, clean water, and essential vitamins and minerals is the best way to prevent livestock poisoning from toxic plants.

Benefits to Humans of Poisonous Plants and Fungi

The benefits that people gain from poisonous plants extend well beyond the pleasure many varieties of beautiful but poisonous house and garden ornamentals, like laburnum and oleander, can bring. From the glycosides of foxglove, used as heart medicines, to the alkaloids of ipecac, used as an emetic to treat poisoning, toxic compounds and poisonous plants applied in appropriate doses provide us with many important medicines. For 80 percent of the world's people, plants are the primary source of medicine, and even in modern industrial societies, over one-quarter of prescriptions are derived at least in part from plants, many of which are potentially toxic.

Pacific yew (*Taxus brevifolia*), for example, is a small forest tree of the Pacific Northwest of North America, which has long been known to have toxic foliage, seeds, and bark. In the late 1960s during a mass screening of plants sponsored by the National Cancer Institute, yew bark was found to contain a potent anticancer drug, called taxol. By the 1980s taxol had undergone extensive clinical trials and became the drug of choice for treating ovarian cancer, previously considered incurable, as well as being used for breast cancer and other forms of cancer.

Another deadly toxin that now has important medicinal applications is derived from a fungus called ergot (*Claviceps* spp.), which grows on grains like rye, wheat, and barley. For many centuries in Europe and elsewhere this fungus, a common contaminant of grain and flour, caused tremendous suffering from chronic poisoning, which produced a range of symptoms from skin ulcers to hallucinations and insanity. In modern medicine, however, ergot is used to stimulate uterine contractions during labor and to control uterine hemorrhaging.

Many other poisonous species have found important applications: strychnine (*Strychnos nux-vomica*) is used in surgery as a relaxant; belladonna's alkaloid, atropine, is used in ophthamology to dilate the pupils of the eyes; opium poppy (*Papaver somniferum*) produces the painkiller morphine; and Madagascar periwinkle (*Cantharanthus roseus*) yields two alkaloids, vincristine and vinblastine, which are used effectively as treatments for childhood leukemia and Hodgkin's disease.

Most people regularly enjoy another beneficial aspect of poisonous plants. Many spices that are used to flavor foods all over the world are actually poisonous if taken in large quantities. For example, nutmeg (*Myristica fragrans*), which grows on trees native to India, Australia, and the South Pacific, contains volatile oils that give it its distinctive aroma and flavour. Harmless in small amounts, in larger doses nutmeg can cause a series of unpleasant effects to the central nervous system, and ten grams can be enough to induce coma, and even death. Mint, black pepper, and cinnamon are further examples of common herbs and spices that are pleasant and beneficial to humans in moderation, but that can be poisonous in large amounts.

Irritants and Allergens

There are also several types of skin irritations caused by plants. Some plants, such as stinging nettle (*Urtica* spp.) and buttercups (*Ranunculus* spp.), have chemicals in their sap or hairs that can be irritating when they come in contact with skin. Some plants contain allergens, causing irritation to the skin of those sensitized to them. Most people find, for example, that they are allergic to poison ivy, and its relatives, poison oak and poison sumac (*Toxicodendron* spp.). While not everyone reacts to these plants, most people do, especially after an initial exposure. Sometimes allergic reactions to these plants are serious enough to lead to hospitalization.

Many people also experience individual allergies to plants and mushrooms that are edible to the general population. Allergies to specific food plants, such as peanuts, lentils, or wheat, can be very serious. In some cases, these otherwise edible species are deadly poisonous allergens for those affected. Plant allergies, including hay fever, can develop at any age and may be alleviated by a program of immunization.

Poisonous Mushrooms

The American fly agaric (*Amanita muscaria*), a common poisonous mushroom.

Mushrooms are part of the diverse kingdom called fungi. Unlike green plants, fungi do not fuel their development, growth, and reproduction with sunlight and carbon dioxide in the process of photosynthesis. Instead, they feed off dead or living plant and animal matter. Mushrooms, which are characterized by a central stalk and rounded cap, can be easily distinguished. While some mushrooms are widely eaten, others can cause sickness if consumed, and some can be fatally toxic even in small amounts. Distinguishing between poisonous and edible mushrooms can be extremely difficult. Sometimes identification can only be verified at the microscopic level and requires the expertise of a mycologist, a person who studies fungi. Wild mushrooms should never be eaten without certain identification. As with poisonous plants, the level of toxicity in mushrooms can vary depending on genetic and environmental factors, and the same species of mushroom that can be eaten in one area may be poisonous under other conditions.

The toxicity of many species of mushrooms is poorly understood, and there is no simple test for determining if a mushroom is poisonous to humans. The symptoms of mushroom poisoning generally include nausea and vomiting, cramps, diarrhea, drowsiness, hallucinations, or even coma. The effects of mushroom poisoning will vary depending on the variety and quantity of the toxins involved, and on the individual reaction of the person who eats the mushroom. The most notorious toxic mushrooms are members of the genus *Amanita*, which includes fly agaric (*A. muscaria*), panther agaric (*A. pantherina*), death cap (*A. phalloides*), and destroying angel (*A. verna*, *A. virosa*). The last two, especially, are the most poisonous mushroom species known. SEE ALSO Alkaloids; Defenses, Chemical; Fungi; Medicinal Plants; Poison Ivy.

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Pollination Biology

Plant pollination is almost as diverse as the plant community itself. Self-pollination occurs in some plant species when the pollen (male part) produced by the anthers in a single flower comes in contact with the stigma (female part) of the same flower or with the stigma of another flower on the same individual. Self-pollination does not allow much modification in the genetic makeup of the plant since the seeds produced by self-pollination create plants essentially identical to the individual producing the seed. A plant population that has all individuals identical in form, size, and growth requirements has little possibility of modifications to allow for change in its environment.

Most plant species have evolved ways to ensure an appropriate degree of interchange of genetic material between individuals in the population, and cross-pollination is the normal type of pollination. In this case flowers are only pollinated effectively if the pollen comes from another plant. Plants benefit most by being pollinated by other individuals because this broadens the genetic characteristics of individual plants. As a result, they are more adaptable to necessary changes.

Fertilization takes place when the pollen comes in contact with the stigma of a flower. Pollen reacts with the stigmatic fluids and germinates, then grows as a tube through the stigma and down the style to the ovary cavity. There the sperm unites with the ovule and develops into a seed.

There are both physical and chemical or genetic barriers to fertilization. Sometimes pollen grains are inhibited from germinating by a chemical imbalance, or germination is controlled genetically. Sometimes there is no genetic barrier but the pollen is simply not placed in the proper position in the flower. This is caused by physical restraints, such as large differences in the length of the stamens and the styles. Some species of plants have long-styled forms and short-styled forms to discourage self-pollination. The shape of the corolla and the positioning of the sexual parts (style and stamens) may also ensure that only an insect of a certain size and shape can pollinate a flower. Most of the pollination syndromes mentioned next involve these features.

Wind Pollination

Perhaps the simplest form of pollination is that of wind pollination, which is common in many of the early spring-flowering trees in temperate areas. The oak (*Quercus* in Fagaceae), maple (*Acer* in Aceraceae), birch (*Betula* in Betulaceae), hickory (*Carya* in Juglandaceae), and many other trees in temperate forests are pollinated by wind-borne pollen. Air currents and moisture in early spring make this a suitably efficient method of pollination because the trees have not yet produced leaves, and flowers are exposed, often in slender **catkin**-type **inflorescences** that dangle with long stigmatic hairs capable of catching the pollen. The corn plant (*Zea mays* in Poaceae) is another wind-pollinated plant. Its long, silky tufts of fiber, which constitute the styles, are well suited to trapping the airborne pollen. Wind pollination is rare in the tropics, perhaps owing to the fact that trees are usually not leafless and wind-borne pollen would not be very efficient. Moreover, heavy daily rains common in the tropics would keep anthers too wet for effective wind pollination. Nevertheless, one type of airborne pollination in the tropics does exist. Understory shrubs in the Urticaceae have anthers that open explosively and throw the pollen into the air sufficiently far to effect at least self-pollination of other inflorescences on the plant.

catkin a flowering structure used for wind pollination

inflorescence an arrangement of flowers on a stalk

Bee pollinating a blossom of a kiwi fruit vine.

Insect Pollination

Plants have coevolved with insects, and each insect pollinator group is closely associated with a particular type of plant. This is called a pollination syndrome. Without even knowing the exact insect that pollinates a plant, the type of insect that will visit the plant can be predicted because of the shape, color, size, and scent of the flower involved.

Bees. Most bees visit flowers that are bilaterally symmetrical (zygomorphic or not round in outline) and have a landing platform on which the bee can be properly oriented for entry. An example is the ordinary household pea plant (*Pisum sativa*) and most other members of the subfamily Papilionoideae of the **legume** family (Leguminosae). Bee flowers tend to have an aroma as well because bees have a good sense of smell. Bees are among the most prevalent of plant pollinators and are remarkably diverse in size and shape. The honeybee is the most obvious example of this pollination syndrome, and the economic importance of the honeybee to fruit and seed production is enormous. Without them and other similar bees, many of our food crops would not exist.

legumes beans and other members of the Fabaceae family

Bees are believed to be intelligent, and some bees return to the same plant on a regular basis (a behavior called trap lining). In such cases, the plants commonly produce just one or a few flowers each day, ensuring that all are pollinated without investing as much energy as it would in a mass-flowering species. Other species produce massive numbers of flowers so that the plant can attract large numbers of pollinators. These are two opposing strategies that accomplish the same goal: to produce seeds for reproduction.

Bees are more likely than other insects to establish a one-to-one pollination system. Many plants produce a special scent that attracts only one or a few different species of bees. This is especially common in orchids and aroids. Some flowers have evolved to produce a "style" that mimics the insect itself in appearance. Most orchids are so dependent on pollination by a single type of bee that they put all of their pollen in a single package (called pollinia) that is picked up by the bee. In the case of the *Catasetum* orchid, the sticky pollinia is forced onto the head of the bee, where it adheres until it in turn is passed onto the style of another plant. This one-chance system, though risky, ensures that all of the pollen load arrives exactly where it is most effective.

Flies. These are less-important pollinators, but they are essential in the pollination of some temperate and many tropical flowering plants. Flies generally visit flowers that smell foul, often with scents of decaying meat or feces. Many tropical aroids (Araceae), including such mammoth plants as *Amorphophallus*, which often produce inflorescences, are pollinated by flies. The skunk cabbage (*Symplocarpus foetidus*), another aroid and one of the earliest plants to flower in the spring (even emerging from snow banks), is pollinated by flies. Flies are seemingly less intelligent than bees and fly pollination syndromes often involve deceit and entrapment. Flies are attracted to foul-smelling plants because they anticipate finding a suitable substance, such as dung or decaying meat on which to lay their eggs. Once inside, however, the flies are unable to leave the inflorescence. In *Aristolochia* (Aristolochiaceae), the corolla tube is folded into a bend with stiff hairlike **appendages** at the base, orientated to allow the fly to enter easily. However, only after the insect has been inside long enough to ensure pollination do the appendages become loose enough to allow the fly to depart the lower part of the corolla. The tropical genus *Dracontium* (Araceae) has no real trap but instead the lower part of the spathe is white or apparently transparent, and the opening is curved so that little light enters. The not-so-intelligent fly tries repeatedly to leave through an opening that does not exist and in the process crashes against the inflorescence to deposit pollen it might be carrying from visiting other flowers.

appendages parts that are attached to a central stalk or axis

Moths and Butterflies. Both have the ability to unroll their long tongues and extend them into long slender flowers. Members of the Asteraceae (Compositae), such as dandelions, sunflowers, goldenrods, and other genera, are usually visited by butterflies during daylight hours. Their moth counterparts usually fly at night and pollinate a different type of tubular flower, ones that are usually white or very pale in color, making the flowers easier to see in the dark, and flowers that produce a sweet-smelling aroma, which also makes locating them easier. Hawk moths have especially long tongues and can pollinate tropical flowers with the corolla tube up to ten inches long. One such flower, *Posoqueria latifolia* (Rubiaceae), has a special arrangement of the stamens that causes them to be held together under tension until the anther mass is touched by the pollinator. At this point, it is released with great force and the stamens then throw a mass of pollen into the face of the pollinator. This pollen mass is carried onto the next flower, where the style is now properly positioned to accept the pollen.

Beetles. Although somewhat rare in temperate areas, this is quite common in the tropics. Beetles often fly at dusk, enter the inflorescence, and stay there until the following evening at dusk. Beetle pollination syndromes often involve thermogenesis, an internal heating of some part of the inflorescence caused by the rapid **oxidation** of starch. The inflorescence of *Philodendron* (Araceae) consists of a leaflike spathe that surrounds the spadix where the flowers are aggregated. The flowers of philodendron are unisexual, with the female flowers aggregated near the base and the male flowers occupying the remainder of the spadix. In most cases, it is the spadix that warms up and the temperature is commonly well above ambient temperature (that of the surrounding air). The elevated temperature is associated with the emission of a sweet scent that helps attract the beetles. Once inside the base of the spathe (the tube portion), the beetles feast on the lipid-rich **sterile** male flowers at the base of the male spadix, and they also often use this space for mating. On the following day, when the beetle is departing, the stamens release their pollen and the beetle departs covered with it. Beetles pollinate many species of palms (Arecaceae), members of the Cyclanthaceae, many Araceae, and even giant tropical water lilies such as *Victoria amazonica*. The skunk cabbage mentioned earlier under fly pollination is also thermogenic, and it is this feature that enables it to melt its way through the snow in the early spring.

oxidation reaction with oxygen

sterile unable to reproduce

Birds and Mammals. Although vertebrate pollinators are not as common as insect pollinators, they do exist, and include birds and mammals. Bird pollination syndromes usually involve colorful, scentless flowers that are designed to attract birds, which have excellent vision but a poor sense of smell. In the western hemisphere, hummingbirds are the most common pollinators, and their typically long tongues mean that hummingbird flowers are typically long and tubular. Many hummingbird-pollinated flowers are either red or have red-colored parts, such as bracts, which attract the bird to the inflorescence. Many tropical members of the Gesneriaceae have yellow rather than red flowers, but the leaves associated with the flowers are heavily marked with red or maroon and are clearly visible to the hummingbird pollinators.

Mammal pollination is rare but is becoming increasingly more well known among tropical animals. White-faced monkeys (*Cebus capuchinus*) are known to pollinate balsa trees (*Ochroma pyramidale* in Bombacaceae) as they search deep in the big tubular flowers for insects. Bats are more common as effective pollinators because they are skilled fliers. Because bats fly at night, the bat pollination syndrome involves pale-colored, usually large, often pendent broadly open tubular flowers, such as *Coutarea hexandra*, a tropical member of the coffee family (Rubiaceae). However, bat pollination syndromes may also involve such plants as *Inga* (Leguminosae), which have many flowers with broad tufts of stamens through which the bat can extend its tongue to forage for pollen or nectar. Some unusual mammal pollinators include giraffes, who are known to pollinate *Acacia* trees with their facial hairs, and lemurs, who pollinate *Strelitzia* in Madagascar. SEE ALSO Breeding Systems; Flowers; Interactions, Plant-Insect; Interactions, Plant-Vertebrate; Reproduction, Fertilization and; Reproduction, Sexual.

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Polyploidy

The analysis of plant and animal cells shows that chromosomes are present in homologous pairs, with each member of the pair carrying very similar or identical genes. In humans, for example, there are forty-six chromosomes, but these can be grouped into twenty-three pairs. This set of twenty-three unique chromosomes is known as the **haploid** number for humans, while the full complement of forty-six chromosomes (two sets of twenty-three) is known as the **diploid** number. Virtually every somatic (non-sex) cell in the body contains the diploid number, while gametes (egg and sperm) contain the haploid number. *Arabidopsis thaliana* (a well-studied model plant) has ten chromosomes in a somatic nucleus, two each of five different types. Like humans, *Arabidopsis* is diploid, with a diploid number of ten and a haploid number of five.

haploid having one set of chromosomes, versus having two (diploid)

diploid having two sets of chromosomes, versus having one (haploid)

While some plants show this diploid pattern of chromosome number, many others show a different pattern, called polyploidy. In this pattern, near-identical chromosomes occur in numbers greater than two, and the number of chromosomes in somatic cells therefore is greater than the diploid number. For instance, the potato has forty-eight chromosomes, but analysis shows that these can be grouped into four sets of twelve, with foursomes (instead of pairs) carrying very similar genes. The potato is said to be tetraploid, which is one form of polyploidy.

Polyploidy does not have to lead to large number of chromosomes, but it often does. For instance, cultivated polyploid plants such as sugarcane are known to have as many as 150 or more chromosomes, while wild plants may have even higher numbers. Most angiosperm (flowering plant) **genomes** are thought to have incurred one or more polyploidization events. Many of the world's leading crops are polyploid.

genome the genetic material of an organism

Chromosome Numbers

A simple **nomenclature** is widely used to provide geneticists with information about chromosome numbers in different organisms. The number of unique chromosomes making up one set is referred to as "x." For example, for humans x = 23, for *Arabidopsis thaliana* x = 5, and for potato x = 12. The number of chromosomes in the gametes of an organism is referred to as "n." For humans n = 23, and for *Arabidopsis thaliana* n = 5. In potato, n = 24, half the total number of chromosomes. Note that for diploid organisms, n = x, meaning the chromosome number of the gamete will be

nomenclatural related to naming or naming conventions equal to the number of unique chromosome types. By contrast, for polyploids, n will be some multiple of x, and the simple formula n/x reflects the number of different sets of chromosomes in the nucleus. For the potato, n/x = 2, indicating that the tetraploid potato carries twice the diploid number of chromosomes. Prefixes for other numbers of chromosomes are tri-(3), tetra-(4), penta-(5), hepta-(7), octo-(8), and so on.

During gamete formation, near-identical chromosomes (homologs) must pair up and undergo recombination (crossing over) before they are segregated into separate gametes. In diploid organisms, this pairing brings together the members of each homologous pair, so that (in *Arabidopsis*, for example), the five chromosomes from one set pair up with the five nearly identical chromosomes from the other set. In polyploid organisms, however, the number of possible pairings is larger. Scientists in fact recognize two different types of polyploidy (autopolyploidy and allopolyploidy, discussed next), based on the tendency of chromosomes from different sets to pair with one another.

A sugar beet plant pulled from a Minnesota sugar beet field. In autopolyploids, such as sugar beets, a member of one set of chromosomes can pair with the corresponding member of any of the other sets.

Autopolyploidy

In autopolyploid (self-polyploid) organisms, such as the potato, the multiple sets of chromosomes are very similar to one another, and a member of one set can pair with the corresponding member of any of the other sets. For the potato, this means that a single chromosome from the first set can pair with up to three other chromosomes. This can lead to multivalent pairing at **meiosis**, with one chromosome pairing with different partners along different parts of its length.

meiosis division of chromosomes in which the resulting cells have half the original number of chromosomes

Further, because any one chromosome can have several different partners, it is impossible to establish allelic relationships. Because of the possible presence of four, six, eight, even ten or more copies of a particular chromosome, genetic analysis of autopolyploids is complex.

Examples of autopolyploids in addition to potato include alfalfa (4x), sugarcane (8-18x), sugar beet (3x), ryegrass (4x), bermuda grass (3-4x), cassava (4x), red clover (4x), Gros Michel banana (3x), apple cultivars (3x), and many ornamentals (3x). Note that many autopolyploids are **biomass** crops, grown for vegetative parts other than seeds. The multivalent pairing associated with autopolyploidy is often not conducive to seed fertility. Many autopolyploids are difficult to obtain seed from and are **propagated** by vegetative clones, such as cuttings.

biomass the total dry weight of an organism or group of organisms

propagate to create more of through sexual or asexual reproduction

Allopolyploidy

Bread wheat (*Triticum aestivum*) is an example of allopolyploidy, in which the multiple sets of chromosomes are not composed of nearly identical chromosomes. In bread wheat, there are 42 chromosomes, divided into six sets of seven chromosomes each. These sets are denoted A, A, B, B, D, and D. While a particular member of A can pair with its homolog in the other A set, it cannot pair with any members of B or D. In effect, bread wheat has three different genomes, which are believed to have arisen from three different diploid ancestors, one each contributing the A, B, and D chromosome sets. These different ancestors are thought to have come together to form the allohexaploid genome of bread wheat. While each ancestor carried many similar genes, they were not arranged in precisely the same way on each chromosome set. Since members of A are not homologous to members of B or D, pairing between the different sets during meiosis is normally not possible.

Therefore, at meiosis in normal bread wheat, there are twenty-one pairs of chromosomes formed, but A chromosomes are paired only with A, B only with B, and D only with D. Thus, despite the presence of six chromosome sets in the same nucleus, each has only one possible pairing partner, and all chromosomes pair as bivalents (one-to-one). Because of strict bivalent pairing, genetic analysis of allopolyploids is similar to that of diploids.

Examples of allopolyploids include cotton (6x), wheat (4x, 6x), oat (6x), soybean (4x), peanut (4x), canola (4x), tobacco (4x), and coffee (4x). Note that many allopolyploids are seed crops. The strict bivalent pairing associated with allopolyploidy is conducive to a high level of seed fertility.

Finally, it is significant that autopolyploidy and allopolyploidy are not mutually exclusive alternatives. Plants can contain multiple copies of some chromosomes and divergent copies of others, a state known as auto-allopolyploidy.

Formation of Polyploids

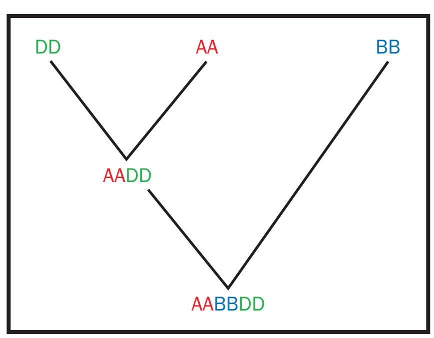
Every plant has the potential to form an autopolyploid at every meiotic cycle, since (as in all sexually reproducing cells) the chromosome number is doubled prior to the first meiotic cycle. Normally, the chromosome number is then reduced by two rounds of chromosome separation during gamete formation. Autopolyploids may be formed when this chromosome separation fails to occur.

Allopolyploids are thought to form from rare hybridization events between diploids that contain different genomes (such as AA and DD diploid wheats). Initially, the **hybrid** of such a cross, with a genetic constitution AD, would be unbalanced, since A and D chromosomes would not pair. As a result, such a hybrid would be **sterile** and would not be genetically stable over time. In rare cases, the AD hybrid may produce a gamete that fails to go through the normal reduction in chromosome number during meiosis, thereby doubling its chromosome number. Such an unreduced gamete may be of genetic constitution AADD, and both A and D chromosomes would have pairing partners, creating a genetically stable polyploid **genotype**:

hybrid a mix of two varieties or species

sterile unable to reproduce

genotype the genetic makeup of an organism



Unreduced gametes can be artificially induced by various compounds, most notably colchicine, which interferes with the action of the meiotic spindle normally responsible for separating chromosomes. Colchicine has been widely used by geneticists to create synthetic polyploid plants, both for experimental purposes and to introduce valuable genes from wild diploids into major crops. Synthetic polyploids developed by humans from wild plants have contributed to improvement of cotton, wheat, peanut, and other crops. One artifically induced polyploid, triticale (which combines the genomes of wheat and rye), shows promise as a major crop itself.

Finally, many crops that are grown for vegetative parts are bred based on crosses between genotypes of different ploidy, which produce sterile progeny. For example, many cultivated types of banana (*Musa* spp.) and Bermuda grass (*Cynodon* spp.) are triploid, made from crosses between a diploid and a tetraploid. In each of these crops, seed production is undesirable for human purposes, and the unbalanced genetic constitution of the triploids usually results in seed abortion. Each of these crops is propagated clonally by cuttings. This is a good example of how humans have applied basic research knowledge to improved quality and productivity of agricultural products.

Occurrence in Plants, Including Economically Important Crops. Many additional plant genomes may have once been polyploid. For example, maize has twenty chromosomes in its somatic nucleus and exhibits strict bivalent pairing—however at the deoxyribonucleic acid (DNA) level, large chromosome segments are found to be duplicated (i.e., contain largely common sets of genes in similar arrangements). In most cases, the duplicated regions no longer comprise entire chromosomes, although they may once have. Other examples of such ancient polyploids include broccoli and turnips. Hints of ancient chromosomal duplications are found in many plants and are particularly well characterized in sorghum and rice. Recent data from DNA sequencing has supported earlier suggestions from genetic mapping that even the simple genome of *Arabidopsis* may contain duplicated chromosomal segments. As large quantitites of DNA sequence information provide geneticists with new and powerful data, it is likely we will discover that many organisms that we think of as diploid are actually ancient polyploids.

Importance in Evolution. Because of the abundance of polyploid plants, it can be argued that the joining of two divergent genomes into a common polyploid nucleus is the single most important genetic mechanism in plant evolution. Geneticists have long debated whether the abundance of polyploid plants simply reflects plant promiscuity or if a selective advantage is conferred by polyploid formation. Plants appear to enjoy greater freedom than animals to interbreed between diverse genotypes, even between genotypes that would normally be considered to be different species. However, one could also envision that the presence of multiple copies of a gene in a plant nucleus offers flexibility to evolve. While mutation (changes in the genetic code) is necessary for evolution, most mutations disrupt the genetic information rather than improve it. In polyploids, if one copy of a gene is disrupted, other copies can still provide the required function—therefore there may be more flexibility to experiment—and allow rare favorable changes to occur.

allele(s) one form of a gene

Autopolyploids may have a different type of genetic buffering. Most autopolyploids are highly heterozygous, with two, three, or more **alleles** represented at any one genetic locus. This may provide the organism with different avenues of response to the demands of different sets of environmental conditions. SEE ALSO Chromosomes; Cotton; Speciation; Wheat.

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Potato

The potato (*Solanum tubersosum*) is one of the world's most productive, nutritious, and tasty vegetables, and it is the fourth most important food worldwide regarding production (following rice, wheat, and corn). It is the most economically valuable and well-known member of the plant family Solanaceae, which contains such foods as tomatoes and peppers, and flowers such as the petunia. The edible tubers of potato are actually swollen underground stems, in contrast to the similarly appearing sweet potatoes, which have swollen roots, and are a member of the separate family Convovulaceae (morning glory family).

Early peoples in the high Andes Mountains of Bolivia and Peru, where many wild potato species grow, likely selected the potato as a food about ten thousand years ago. This is a time when many crops were believed to have been selected in Andean South America, and dried potato remains date from about seven thousand years ago from caves in Central Peru. Wild potato species have a geographic range from the southwestern United States to south-central Chile. There is much controversy regarding the number of wild potato species, from perhaps only one hundred to over two hundred.

The potato was not introduced into Europe until the late sixteenth century, where it was only slowly accepted as a food, and even then only by the poor. The potato is infected by many diseases and requires a lot of care. The fungal disease potato late blight was the cause of the devastating Irish potato famine that began in 1846. The famine killed more than one million people and stimulated the huge immigration of Irish people to continental Europe and the United States. SEE ALSO Economic Importance of Plants; Potato Blight; Solanaceae.

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Potato Blight

Potato blight (or potato late blight) is caused by a mildewlike fungus called *Phytophthora infestans* that can infect the potato foliage and its tubers. Although *P. infestans* is best known as a **pathogen** of the potato, this fungus also attacks the tomato and a number of other plants belonging to the family Solanaceae.

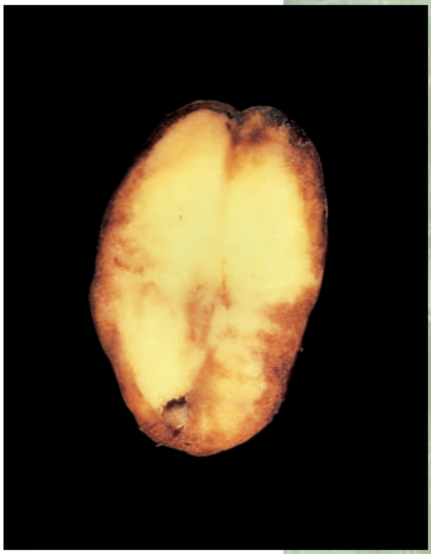
pathogen disease-causing organism

History

This disease first came to the attention of the world in the 1840s, when it suddenly appeared in Europe and caused the disastrous Irish potato famine. From Europe, the fungus spread all over the world. At first it was thought that the blight was simply due to rainy, cool weather, which caused the potato foliage to turn black and die. In 1863, a German scientist, Anton deBary, proved that *P. infestans* was the cause of the disease, and through his pioneering work, deBary established the base for a new science: plant pathology.

sporulate(s) to produce or release spores

In 1884 in France, a fungicide spray containing copper sulphate and lime, called Bordeaux mixture, was discovered to be an effective means of controlling potato blight when applied to the foliage. This was the first time a plant disease was controlled by protective spraying. During the past fifty years hundreds of chemical fungicides have been developed for the control of potato blight. In the early twenty-first century, the potato crop receives more chemicals annually than any other food plant that we grow. The annual losses due to potato late blight, including both the direct losses in yield and the expense of chemical control, amount to billions of dollars a year.



A potato diseased with potato late blight.

The Disease

P. infestans passes the winter in infected seed tubers kept in potato storages or in the soil of the potato field to be planted. As the new potato crop becomes established during a cool, wet season, the fungus emerges, **sporulates**, and attacks both the foliage and the tubers. If this favorable weather continues, the potato plants can be completely destroyed.

Unfortunately, almost all commercial potato varieties are susceptible to blight and must be protected by spraying with chemical fungicides. Although the potato has emerged as one of the four major food crops in the world during the last few centuries (rice, wheat, and corn being the others), the need for expensive protective spraying has tended to confine its major impact to the more prosperous, industrialized countries of the world. It is urgent that we initiate and support a long-term program to enable the potato to continue and expand its contribution to the nutrition of a growing world population.

An obvious solution for this disease problem, which has caused so much expense and uncertainty in world potato production, is to incorporate a durable late blight resistance in commercially acceptable potato varieties. A high level of this blight resistance has been found in a number of wild potato species in Mexico, which is now recognized as the place of origin of *P. infestans.* These resistant wild potatoes have evolved there, surviving for thousands of years, in a climate favorable for an annual battle with the blight fungus.

Research programs in many countries are now trying to develop commercially acceptable potato varieties with this durable resistance. These resistant potato varieties will not only save the farmer the cost of applying the expensive fungicides, but will provide them with greater security in the production of a good crop of potatoes. Perhaps even more important, for the first time the potato would be available as a basic food crop to many millions of subsistence farmers in developing countries. Today these farmers cannot grow the potato because they do not have the resources needed for the purchase of expensive chemicals used for the control of potato blight.

Today there is an increasing global concern over the quality of the environment. A substantial reduction in the use of agricultural chemicals is considered to be an important step if we are to make progress in improving the environment. The worldwide use of blight-resistant potato varieties would be an important contribution to this program. SEE ALSO BREEDING; ECONOMIC IMPORTANCE OF PLANTS; GENETIC ENGINEERING; INTERACTIONS, PLANT-FUNGAL; PATHOGENS; POTATO.

John S. Niederhauser

Propagation

Plant propagation simply means “making more plants.” Reproducing plants from seeds is called sexual propagation. If plant parts other than seeds are used to reproduce a plant, the method is known as asexual propagation. Many ornamental trees, flowering shrubs, foliage plants, and turf grasses are propagated by asexual means. Asexual propagation of plants is generally accomplished by one of three methods: cuttings, grafting, and tissue culture or micropropagation.

Asexual Propagation

Asexual propagation is easy to accomplish, inexpensive, and often requires no special equipment. Asexual techniques are used because larger plants can be produced in a shorter period of time. If a plant does not form **viable** seeds, or if the seeds are difficult to germinate, asexual methods may

viable able to live or to function

Plantlets of a Mother-of-Thousands plant can be detached and potted separately.

be the only way to reproduce the species. Asexual propagation produces clones, and, consequently, all new plants will resemble the parent plant, a benefit for growers who want to multiply and sell a unique plant.

Since the newly propagated clones are genetically identical, they respond to the environment in similar ways. This uniformity makes culture and production easy. However, it can be a problem if a pest or disease attacks the crop. Asexually propagated clones may all be vulnerable to the attackers, which could wipe out the crop.

Cuttings. Asexual plant propagation using cuttings involves removing certain plant parts and allowing each cut part to become a new plant. Common plant parts used as cuttings include stems, leaves, leaf buds, and roots. When exposed to proper environmental conditions and appropriate cultural practices, cuttings form a root system and new foliage. New roots or shoots are termed **adventitious** growth.

adventitious arising from secondary buds

Stem cuttings are one of the easiest and least-expensive methods of plant propagation. Most species will make roots in several weeks. Rooted cuttings are then easily grown to marketable size. Stem cuttings can be classified into groups according to the nature of the plant wood used: hardwood and softwood.

Hardwood stem cuttings are taken from mature **dormant** branches in late fall or early winter. If the species is deciduous, cuttings should be leafless. A 15- to 20-centimeter section of stem with at least three buds is used.

dormant inactive, not growing

The base of the cutting is cut at a slant to expose a larger area for rooting and to create a distinction between the cutting top and base. For evergreen species, leaves on the lower half of the cutting are stripped off. Then the base is dipped in a root-promoting hormone, either a powder or liquid. The cutting is inserted (about one-half its length) into a moist rooting medium composed of peat mixed with vermiculite or sand. Cuttings should be kept moist at a temperature favorable for optimum growth and development, depending on the plant species. Adequate light is necessary for root formation, but cuttings should never be placed in direct sunlight. Sometimes protected trays of hardwood cuttings are kept outside through mild winters, and they root as temperatures rise in the spring.

succulent fleshy and moist

node branching site on a stem

Stem cuttings of softwood generally root more easily than hardwood but require more attention and equipment. Softwood cuttings are usually 7.5 to 13 centimeters long with two or more nodes. They are usually made in late spring, using the **succulent** mature spring growth of deciduous or evergreen plants. Mature shoots, but not old woody stems, are desirable. A slanted base cut is made just below a **node,** and leaves on the lower half of the cutting are removed. Bases are treated with rooting stimulant before being placed into loose rooting mix. Softwood cuttings require high humidity, which can be achieved through the use of plastic tents, misting systems, and/or fogging. Temperature should be closely observed during rooting. Most species root best between temperatures of 25°C and 30°C at the base, with cooler temperatures for foliage. Having the base warmer than the tip promotes root growth before new top growth begins. Roots form in two to five weeks.

petiole the stalk of a leaf, by which it attaches to the stem

Leaf cuttings are another method of asexual propagation. In this process, an entire leaf (leaf blade plus **petiole**), the leaf blade only, or just a portion of the blade can be used to produce another plant. Cut surfaces may be treated with rooting hormones. High relative humidity and warm soil temperature will speed adventitious root formation. The soil mix should be loose but damp. Using the leaves allows the reproduction of more new plants than is possible with stem cuttings: sometimes more than one new plant forms from each leaf. Many leaves can fill a shallow tray. On one greenhouse table hundreds of plants can be reproduced.

axillary bud the bud that forms in the angle between the stem and leaf

Leaf-bud cuttings are basically the same as leaf cuttings, except the leaf is left attached to a short piece of stem with its healthy **axillary bud.** The cut stem surface can be treated with root-promoting compound. The cuttings are inserted in a rooting medium with the bud about 1.4 centimeters below the surface. High humidity and optimum temperature will speed rooting.

suckers naturally occuring adventitious shoots

Root cuttings when buried and kept warm will produce adventitious shoots. Root cuttings consist of roots less than 1 centimeter in diameter cut into short lengths, 2.5 to 8 centimeters long. These are placed horizontally on the rooting media and covered with a 1.3 centimeter layer of fine soil or sand. The rooting medium is kept moist; it is important not to let it dry out. After the cuttings have developed adventitious roots and shoots, they can be transplanted for further growth. Plants that naturally form **suckers** at the base are good candidates for cloning through root cuttings.

Grafting. The process of joining plants together in such a way that they will unite and grow as one plant is commonly referred to as grafting. The

Workers prepare graft clones of cacao leaves. The tips are dipped into an enzyme and planted for rooting. Through cloning, all of the cacao on this Ecuadoran plantation is of the same variety and will be used for chocolate production.

part that becomes the upper portion or top of the graft is termed the scion, and the lower portion is called the rootstock or stock. The general process of joining plants is referred to as grafting. When the scion part is just a bud, the operation is called budding. Grafting is a method of plant propagation that is thousands of years old, and there are many methods. All of them involve fastening fresh woody stems together, excluding light, preventing the stems from drying out, and training the new growth.

The advantages of grafting and budding are numerous. Many common fruits such as apples, pears, peaches, and walnuts cannot be satisfactorily propagated by cuttings. In order to meet market demands, the grower is forced to use grafting and budding as a means of reproduction. In other instances, certain rootstocks have desirable characteristics such as resistance to soil diseases, dwarfism (reduced plant size), cold hardiness, and vigor. Through grafting it is possible to combine desirable qualities that are found in these rootstocks with desirable flowering and fruit qualities that are found on different scion varieties. Some stocks, by imparting a dwarf quality to the scion, reduce tree size. This allows smaller trees to be planted closer together in orchards, increasing crop yield per unit of space.

Grafting also enables the agriculturalist to change the variety of established plants. This technique is often beneficial in apple orchards. An older variety may be in ill health or no longer in demand. As long as the new scion wood is compatible, the established variety can serve as a rootstock and a new variety can be grafted onto old trees without digging up the entire orchard.

hybrid a mix of two varieties or species

The fruits of grafted plants are always of the scion variety: they are not combinations or **hybrids** of the scion and stock varieties. When closely related plants are grafted, most will continue their growth as a single plant. When the scion and rootstock unite and continue to grow as one plant, producing for many years, the graft is said to be compatible. When unrelated plants are grafted, the usual result is failure; the graft is incompatible. Certain combinations of scion and rootstock might grow and continue in a normal manner for several weeks only to have the scion die. Trees that are advertised as being "fruit salad" trees have five or six different scion varieties grafted onto one stock. Typically several of these scions are incompatible and will die off.

Tissue Culture or Micropropagation. If they are kept under a proper environment, plants can reproduce themselves even from very small parts. When the removed part is not much more than a few cells, the process is called tissue culture or micropropagation. The small section that is removed is termed the explant. It may be taken from the roots, leaves, stem, or growing tips. In tissue culture, the explant is put into nutrient solution in a test tube, petri dish, or other container and kept in a clean, bright environment. The artificial medium contains all the nutrients, food, and hormones to help the explant create new cells. Roots or shoots may emerge within a few weeks. Each rooted explant can then be divided, and each smaller portion cultured again, rapidly multiplying the number of plants.

The advantages of tissue culture or micropropagation include the following:

- All the plants produced through tissue culture are clones of the parent plant.
- Because the explants and lab containers are so small, micropropagation can yield many thousands of plants in one laboratory or greenhouse.
- Many clones can be multiplied relatively quickly.
- The smallest part of the growing tip (not much more than a few cells) is often free from viruses that may be present throughout the rest of the plant. By cloning this very small **meristematic** portion, a worker can reproduce the plant virus-free.

meristematic related to cell division at the tip

- Shipping many plants in small sterile containers is easier and safer than shipping larger plants with soil and watering problems.
- Many countries have laws that do not allow soil from other countries to cross their borders. Because these little plants in plastic containers do not have any soil, trade between these countries is not restricted.

Disadvantages or problems associated with tissue culture include the high cost of laboratory setup, the skill needed by workers, and the cost of environmental controls. Problems can also result from the lack of one of the important requirements for performing tissue culture or micropropagation successfully: a super-clean work area, correct medium, and proper environment. Laboratories or companies specializing in tissue culture often have very sophisticated equipment to ensure clean conditions. It is most important to keep bacteria and fungal spores away from the explant and nutrient medium. The explant surface is washed with a weak bleach solution to remove pathogens (bacteria or fungal spores that can spread in the container). Washing hands, cleaning tools, and surfaces with alcohol, and working quickly will prevent the contamination of containers and nutrient medium. Special nutrient mixes can be purchased from a commercial source or created from ingredients in a lab. The mix contains sugar, which supplies carbon to the tiny explant while it is unable to use the CO_2 in the air for photosynthesis. Also required are vitamins and nutrients that a healthy plant absorbs through its roots. Hormones stimulate cell division and the formation of roots and shoots. Light is necessary for the plant to develop roots and shoots. Temperatures must be in the range of 20 to 27°C.

There are four stages of the tissue culture or micropropagation procedure:

1. establishment and stabilization, when the small explant is inserted into the container (onto the medium) and survives the initial transplant;
2. shoot multiplication, when each explant expands into a cluster of microshoots and each cluster is divided and re-cultured to increase numbers;
3. pretransplant or in-vitro rooting, when the explant is transferred to another media mix that stimulates roots to form inside the container (in vitro means "in glass"); and
4. transplanting, acclimation, and more rooting, when the explant is transplanted into a clean potting mix and moved into a warm bright greenhouse where it will begin independent photosynthesis and establishment. SEE ALSO Horticulture; Reproduction, Asexual; Reproduction, Sexual; Tissue Culture.

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Psychoactive Plants

compound a substance formed from two or more elements

Compounds in some plants can have an overwhelming effect on the central nervous system. Plants containing those **compounds** are thus known as mind-altering (active) or psychoactive plants. Their effects may be separated into hallucinogenic, stimulating, or depressing properties depending on the plant used and the present compounds, which are usually secondary metabolites. A few plants, however, have major multiple effects based on one or more compounds present, such as tobacco containing nicotine, which can be both stimulating and depressing.

Three points are worth keeping in mind about these plants. First, psychoactive drugs have been used in many cultures throughout human history. Their use has often been highly ritualized (especially true for hallucinogens) and incorporated into religions or mystical ceremonies in such a way that the novice is guided and protected by more experienced members of the ritual. Such practices have tended to minimize the potential for abuse inherent in psychoactive drugs. Second, variations in the concentrations of the active ingredients in plants make the dosing of psychoactive drugs more art than science for even the most experienced user. Last, most of the substances discussed are illegal to possess or use in the United States or Canada.

Plants Having Hallucinogenic Effects

Most hallucinogens are plant secondary metabolic compounds. In amounts that are nontoxic, hallucinogens produce changes in perception, thought, and mood without causing major disturbances of the autonomic nervous system (the system regulating the activity of the heart, smooth muscles, and glands). The psychic changes and abnormal states of consciousness induced by hallucinogens differ from ordinary experiences. Hallucinogenic users forsake the familiar world and, in full consciousness, embrace a dreamlike world operating under different standards, strange dimensions, and in different times. These compounds are a means of escaping from reality as it is commonly understood. They are not physically addicting, although dependency may develop. A few examples are provided to illustrate these properties.

Peyote. The aboveground part of the cactus peyote (*Lophophora williamsii*, family Cactaceae) is chewed or a decoction (boiled in water) is drunk. Ingestion produces nausea, chills, and vomiting, and in most users anxiety and a dislocation of visual perspective. These symptoms are followed by a clarity and intensity of thought, the motion of brilliant-colored visions, and an exaggerated sensitivity to sound and other sense impressions. Activity is centered around the alkaloid mescaline.

Nutmeg and Mace. Powdered nutmeg or mace (*Myristica fragrans*, family Myristicaceae) is taken orally in hot water or sniffed. Unpleasant side ef-

The lush foliage of an *Ayahuasca* vine in the Amazon Basin in Peru. Its leaves are used in a purging and hallucinogenic beverage.

fects almost always occur, and include headache, dizziness, nausea, sickening hangovers, and tachycardia (rapid heart beat). There are feelings of detachment, visual and auditory hallucinations, and sensations of floating or flying and separation of limbs from the body. The latter typifies the more toxic hallucinogens, and the volatile oils elemicin and myristicin are thought to be involved.

Ayahuasca. The bark of the woody vine *Ayahuasca* (*Banisteriopsis caapi*, family Malpighiaceae) often together with leaves of certain *Psychotria* spp., is boiled and the decoction drunk in many parts of tropical South America as a major hallucinogenic beverage. Shortly after ingesting, vomiting occurs, feelings of cold and spiral-flying sensations associated with nausea take place, and visions of blue-masked specters (often assuming grotesque forms) and alarming animals (e.g., boa constrictors) are seen. During this time, hearing is distorted and the individual becomes acutely sensitive. Later, motor coordination is reduced to staggering, the body is hot and sweaty, and salivation and spitting are continuous. If sufficient active compounds have been absorbed, the sensation of flying occurs while observing beautiful and often spectacular sights, a time when exultation sweeps the body, and all physical discomforts are forgotten. Objects and scenes are vividly colored in bright but natural colors. Very few participants reach the ultimate in psychoactive experience, reported telepathic sensitivity. The active ingredients include N,N-dimethyltryptamine (DMT) and the alkaloids harmine, harmaline, and others.

Ololioqui. The morning glories *Ololioqui* (*Ipomoea violacea* and *Rivea corymbosa*, family Convolvulaceae) are associated with Aztec and other Mexican Indian divinations and human sacrifices. Ingesting infusions and decoctions from powdered seeds induces delirium, hypnotic effects, and heightened visual perception. D-lysergic acid amide is the active hallucinogen.

Angel's trumpet and jimsonweed. Ingesting or smoking the seeds, flowers, and leaves of Angel's trumpet and jimsonweed (*Brugmansia* spp. and *Datura* spp., respectively; family Solanaceae) will severely intoxicate the user, resulting in fever, flushing, dilated pupils, fast heart rate and pulse, and sometimes aggressive and violent behavior. In addition, a state of confused delirium may occur, which can be dangerous to the individual if not restrained. The usual hallucinations appear as a parade of material objects, sports cars and flowers, for example, in their simple colors. The vision-inducing hallucinogens are tropane alkaloids, particularly scopolamine.

Marijuana. Smoked or ingested, the resin from floral and leaf glands of marijuana (*Cannabis sativa*, family Cannabaceae) can cause visionary hallucinations that are often pleasant, with sexual overtones. Its most universal effect is as an euphoric, the user having a feeling of well-being and exaltation. Dangers resulting from heavy smoking exist to bronchial tracts and lungs, and prolonged use can cause personality changes that may lead to a marked deterioration in what is normally considered good mental health. The active compound is one or more resinous tetrahydrocannabinols.

Plants Having Stimulating Effects

Stimulants have long been enjoyed by humans, for they give a sense of well-being and exhilaration, self-confidence, and power, and they alleviate fatigue and drowsiness. For most, depending on the dose, there is a price to be paid for their use: increased agitation, apprehension, and anxiety, mild mania (flight of ideas), as well as increased tolerance and often dependency. All of the stimulants described next have these positive and negative effects, except tobacco.

Coca. Native to and widely cultivated in the Andes of South America, the coca plant (*Erythoxylum coca*, family Erythroxylaceae) has a long history of use as a stimulant and hunger depressant. Stimulation is due to the tropane alkaloid cocaine found in leaves that are chewed or ingested as a beverage. Cocaine is readily extracted from leaves and the pure compound can be sniffed, smoked, or injected. Addiction to cocaine as a recreational drug is widespread.

Chat or Khat. Widely found native of the highlands of northeastern Africa and the adjacent Arabian peninsula, chat or khat (*Catha edulis*, family Celastraceae) is also cultivated in these regions. Chat leaves are chewed fresh, giving varying degrees of exhilaration and stimulation. The active ingredient is the alkaloid cathinone, and to lesser degrees norephedrine and norpseudoephedrine derived by enzymatic reduction from the unstable cathinone. Dependency on chat is common.

Coffee, Tea, Chocolate, and Holly. Coffee (*Coffea arabica*, family Rubiaceae), tea (*Camellia sinensis*, Theaceae), chocolate (*Theobroma cacao*, Sterculiaceae), and holly (*Ilex paraguariensis*, Aquifoliaceae) are stimulating beverages common throughout the world. All possess one or more of the xanthine alkaloids: caffeine, theobromine, and theophylline. Of the three, caffeine is the most stimulating.

Tobacco. Tobacco (*Nicotiana tabacum*, family Solanaceae) leaves are smoked or chewed to act as a stimulant, depressant, or tranquilizer. Tobacco with the addictive alkaloid nicotine is perhaps the most physiologically damaging substance generally used by humans. Its use is a direct cause of lung and other cancers, coronary artery disease, and emphysema.

Plants Having Depressant Effects

By depressing the central nervous system, a number of secondary metabolites produce the effects of euphoria and well-being with sedation, including calming and tranquilizing, followed by sleep. Coma ending with death from respiratory failure can result as drug doses increase to higher levels. When controlled, all are enormously useful in medicine, but all are subject to major abuse and often lead to addiction.

Kava. Kava (*Piper methysticum*, family Piperaceae) roots and rhizomes are chewed or grated and prepared in cold water, which, when ingested, produce euphoria. This is the common depressant of the South Pacific region. Larger doses can result in impaired vision, lack of muscle coordination, and hypnosis. The active compounds are pyrones.

Opium Poppy. The opium poppy (*Papaver somniferum*, family Papaveraceae) has been long in cultivation and is probably native to western Asia. Unripe fruit capsules are incised after the petals fall and the milky exudate is air dried and molded into a gummy substance known as opium. Opium contains many compounds, but the alkaloids morphine and codeine are its most important depressants. From morphine, the **illicit** drug heroin is produced. Morphine effectively reduces pain and is a strong hypnotic, whereas codeine is widely used as a sedative to allay coughing. All are addictive with serious withdrawal symptoms. SEE ALSO ALKALOIDS; CANNABIS; COCA; ETHNOBOTANY; MEDICINAL PLANTS; OPIUM POPPY; TOBACCO.

illicit illegal

Walter H. Lewis

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Quantitative Trait Loci

Quantitative traits are characteristics such as plant height or seed size, which can vary over a large range of possible values. The chromosomal regions controlling variation in a quantitative trait are known as quantitative trait loci.

The set of hereditary material transmitted from parent to offspring is known as the genome. It consists of molecules of deoxyribonucleic acid (DNA) arranged on chromosomes. Genetic markers are neutral DNA sequences that have no effect on an individual's physical appearance but are identifiable in the laboratory. Using statistical methods, the location of markers within an organism's genome can be estimated. The linear ordering of markers literally acts as a road map across the organism's genetic composition. This information allows a plant breeder to associate (link) an inherited observable characteristic such as seed size with a marker. This makes it possible to identify progeny possessing that characteristic (even before it shows) by determining whether the individual has that particular genetic marker. In plant breeding applications, the location of specific regions of a genome responsible for controlling quantitative variation of a trait, such as seed size, is of increasing concern to those interested in crop performance.

Quantitative traits may be affected by many loci. A statistical representation (mathematical equation) of the quantitative trait describes the genetic variation in each region of the genome. Quantitative trait loci (QTL) analysis provides information for selectively manipulating genetic components of a trait. The basis of QTL detection, regardless of the crop to which it is applied, is the identification of associations between genetically determined phenotypes (physical characteristics) and genetic markers (genetic characteristics).

The emergence of high-resolution molecular marker technologies is likely to facilitate large-scale QTL analyses. QTL studies provide a first step in understanding the genetics that underlie the expression of quantitative traits. The hope for future research is that the foundation and knowledge gained from QTL research will aid our understanding of the biological function of genes, thus continuing the long history between the fields of genetics and statistics. SEE ALSO BREEDER; REEDING; GENETIC ENGINEER; MOLECULAR PLANT GENETICS.

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Glossary

abiotic nonliving

abrade to wear away through contact

abrasive tending to wear away through contact

abscission dropping off or separating

accession a plant that has been acquired and catalogued

achene a small, dry, thin-walled type of fruit

actinomycetes common name for a group of Gram-positive bacteria that are filamentous and superficially similar to fungi

addictive capable of causing addiction or chemical dependence

adhesion sticking to the surface of

adventitious arising from secondary buds, or arising in an unusual position

aeration the introduction of air

albuminous gelatinous, or composed of the protein albumin

alkali chemically basic; the opposite of acidic

alkalinization increase in basicity or reduction in acidity

alkaloid bitter secondary plant compound, often used for defense

allele one form of a gene

allelopathy harmful action by one plant against another

allopolyploidy a polyploid organism formed by hybridization between two different species or varieties (*allo* = other)

alluvial plain broad area formed by the deposit of river sediment at its outlet

amended soils soils to which fertilizers or other growth aids have been added

amendment additive

anaerobic without oxygen

analgesic pain-relieving

analog a structure or thing, especially a chemical, similar to something else

angiosperm a flowering plant

anomalous unusual or out of place

anoxic without oxygen

antenna system a collection of protein complexes that harvests light energy and converts it to excitation energy that can migrate to a reaction center; the light is absorbed by pigment molecules (e.g., chlorophyll, carotenoids, phycobilin) that are attached to the protein

anthropogenic human-made; related to or produced by the influence of humans on nature

antibodies proteins produced to fight infection

antioxidant a substance that prevents damage from oxygen or other reactive substances

apical meristem region of dividing cells at the tips of growing plants

apical at the tip

apomixis asexual reproduction that may mimic sexual reproduction

appendages parts that are attached to a central stalk or axis

arable able to be cultivated for crops

Arcto-Tertiary geoflora the fossil flora discovered in Arctic areas dating back to the Tertiary period; this group contains magnolias (*Magnolia*), tulip trees (*Liriodendron*), maples (*Acer*), beech (*Fagus*), black gum (*Nyssa*), sweet gum (*Liquidambar*), dawn redwood (*Metasequoia*), cypress (*Taxodium*), and many other species

artifacts pots, tools, or other cultural objects

assayer one who performs chemical tests to determine the composition of a substance

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

attractant something that attracts

autotroph "self-feeder"; any organism that uses sunlight or chemical energy

auxin a plant hormone

avian related to birds

axil the angle or crotch where a leaf stalk meets the stem

axillary bud the bud that forms in the angle between the stem and leaf

basipetal toward the base

belladonna the source of atropine; means "beautiful woman," and is so named because dilated pupils were thought to enhance a woman's beauty

binomial two-part

biodirected assays tests that examine some biological property

biodiversity degree of variety of life

biogeography the study of the reasons for the geographic distribution of organisms

biomass the total dry weight of an organism or group of organisms

biosphere the region of the Earth in which life exists

biosynthesis creation through biological pathways

biota the sum total of living organisms in a region of a given size

biotic involving or related to life

bryologist someone who studies bryophytes, a division of nonflowering plants

campanulate bell-shaped

capitulum the head of a compound flower, such as a dandelion

cardiotonic changing the contraction properties of the heart

carotenoid a yellow-colored molecule made by plants

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

catastrophism the geologic doctrine that sudden, violent changes mark the geologic history of Earth

cation positively charged particle

catkin a flowering structure used for wind pollination

centrifugation spinning at high speed in a centrifuge to separate components

chitin a cellulose-like molecule found in the cell wall of many fungi and arthropods

chloroplast the photosynthetic organelle of plants and algae

circadian "about a day"; related to a day

circumscription the definition of the boundaries surrounding an object or an idea

cisterna a fluid-containing sac or space

clade a group of organisms composed of an ancestor and all of its descendants

cladode a modified stem having the appearance and function of a leaf

coalescing roots roots that grow together

coleoptile the growing tip of a monocot seedling

collenchyma one of three cell types in ground tissue

colonize to inhabit a new area

colony a group of organisms inhabiting a particular area, especially organisms descended from a common ancestor

commensalism a symbiotic association in which one organism benefits while the other is unaffected

commodities goods that are traded, especially agricultural goods

community a group of organisms of different species living in a region

compaction compacting of soil, leading to the loss of air spaces

complex hybrid hybridized plant having more than two parent plants

compound a substance formed from two or more elements

concentration gradient a difference in concentration between two areas

continental drift the movement of continental land masses due to plate tectonics

contractile capable of contracting

convective uplift the movement of air upwards due to heating from the sun

coppice growth the growth of many stems from a single trunk or root, following the removal of the main stem

cortical relating to the cortex of a plant

covalent held together by electron-sharing bonds

crassulacean acid metabolism water-conserving strategy used by several types of plants

crop rotation alternating crops from year to year in a particular field

cultivation growth of plants, or turning the soil for growth of crop plants

crystallography the use of x-rays on crystals to determine molecular structure

cuticle the waxy outer coating of a leaf or other structure, which provides protection against predators, infection, and water loss

cyanide heap leach gold mining a technique used to extract gold by treating ore with cyanide

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

cyanogenic giving rise to cyanide

cytologist a scientist who studies cells

cytology the microscopic study of cells and cell structure

cytosol the fluid portion of a cell

cytostatic inhibiting cell division

deductive reasoning from facts to conclusion

dendrochronologist a scientist who uses tree rings to determine climate or other features of the past

dermatophytes fungi that cause skin diseases

desertification degradation of dry lands, reducing productivity

desiccation drying out

detritus material from decaying organisms

diatoms hard-shelled, single-celled marine organisms; a type of algae

dictyosome any one of the membranous or vesicular structures making up the Golgi apparatus

dioicous having male and female sexual parts on different plants

diploid having two sets of chromosomes, versus having one set (haploid)

dissipate to reduce by spreading out or scattering

distal further away from

diurnal daily, or by day

domestication the taming of an organism to live with and be of use to humans

dormant inactive, not growing

drupe a fruit with a leathery or stone-like seed

dynamical system theory the mathematical theory of change within a system

ecophysiological related to how an organism's physiology affects its function in an ecosystem

ecosystem an ecological community and its environment

elater an elongated, thickened filament

empirical formula the simplest whole number ratio of atoms in a compound

emulsifier a chemical used to suspend oils in water

encroachment moving in on

endemic belonging or native to a particular area or country

endophyte a fungus that lives within a plant

endoplasmic reticulum the membrane network inside a cell

endosperm the nutritive tissue in a seed, formed by the fertilization of a diploid egg tissue by a sperm from pollen

endosporic the formation of a gametophyte inside the spore wall

endosymbiosis a symbiosis in which one organism lives inside the other

Enlightenment eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

entomologist a scientist who studies insects

enzyme a protein that controls a reaction in a cell

ephemeral short-lived

epicuticle the waxy outer covering of a plant, produced by the epidermis

epidermis outer layer of cells

epiphytes plants that grow on other plants

escarpment a steep slope or cliff resulting from erosion

ethnobotanist a scientist who interacts with native peoples to learn more about the plants of a region

ethnobotany the study of traditional uses of plants within a culture

euglossine bees a group of bees that pollinate orchids and other rain-forest plants

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

extrafloral outside the flower

exudation the release of a liquid substance; oozing

facultative capable of but not obligated to

fertigation application of small amounts of fertilizer while irrigating

filament a threadlike extension

filamentous thin and long

flagella threadlike extension of the cell membrane, used for movement

flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

florigen a substance that promotes flowering

floristic related to plants

follicle sac or pouch

forbs broad-leaved, herbaceous plants

free radicals toxic molecular fragments

frugivous feeding on fruits

gametangia structure where gametes are formed

gametophyte the haploid organism in the life cycle

gel electrophoresis a technique for separating molecules based on size and electrical charge

genera plural of genus; a taxonomic level above species

genome the genetic material of an organism

genotype the genetic makeup of an organism

germplasm hereditary material, especially stored seed or other embryonic forms

globose rounded and swollen; globe-shaped

gradient difference in concentration between two places

green manure crop planted to be plowed under to nourish the soil, especially with nitrogen

gymnosperm a major group of plants that includes the conifers

gynoecium the female reproductive organs as a whole

gypsipherous containing the mineral gypsum

hallucinogenic capable of inducing hallucinations

haploid having one set of chromosomes, versus having two (diploid)

haustorial related to a haustorium, or food-absorbing organ

hemiterpene a half terpene

herbivore an organism that feeds on plant parts

heterocyclic a chemical ring structure composed of more than one type of atom, for instance carbon and nitrogen

heterosporous bearing spores of two types, large megaspores and small microspores

heterostylous having styles (female flower parts) of different lengths, to aid cross-pollination

heterotroph an organism that derives its energy from consuming other organisms or their body parts

holistic including all the parts or factors that relate to an object or idea

homeotic relating to or being a gene that produces a shift in structural development

homology a similarity in structure between anatomical parts due to descent from a common ancestor

humus the organic material in soil formed from decaying organisms

hybrid a mix of two varieties or species

hybridization formation of a new individual from parents of different species or varieties

hydrological cycle the movement of water through the biosphere

hydrophobic water repellent

hydroponic growing without soil, in a watery medium

hydroxyl the chemical group -OH

hyphae the threadlike body mass of a fungus

illicit illegal

impede to slow down or inhibit

inert incapable of reaction

inflorescence a group of flowers or arrangement of flowers in a flower head

infrastructure roads, phone lines, and other utilities that allow commerce

insectivorous insect-eating

intercalary inserted; between

interspecific hybridization hybridization between two species

intertidal between the lines of high and low tide

intracellular bacteria bacteria that live inside other cells

intraspecific taxa levels of classification below the species level

intuiting using intuition

ionic present as a charged particle

ions charged particles

irreversible unable to be reversed

juxtaposition contrast brought on by close positioning

lacerate cut

Lamarckian inheritance the hypothesis that acquired characteristics can be inherited

lamellae thin layers or plate-like structure

land-grant university a state university given land by the federal government on the condition that it offer courses in agriculture

landrace a variety of a cultivated plant, occurring in a particular region

lateral to the side of

legume beans and other members of the Fabaceae family

lignified composed of lignin, a tough and resistant plant compound

lineage ancestry; the line of evolutionary descent of an organism

loci (singular: locus) sites or locations

lodging falling over while still growing

lytic breaking apart by the action of enzymes

macromolecule a large molecule such as a protein, fat, nucleic acid, or carbohydrate

macroscopic large, visible

medulla middle part

megaphylls large leaves having many veins or a highly branched vein system

meiosis the division of chromosomes in which the resulting cells have half the original number of chromosomes

meristem the growing tip of a plant

mesic of medium wetness

microfibrils microscopic fibers in a cell

micron one millionth of a meter; also called micrometer

microphylls small leaves having a single unbranched vein

mitigation reduction of amount or effect

mitochondria cell organelles that produce adenosine triphosphate (ATP) to power cell reactions

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

molecular systematics the analysis of DNA and other molecules to determine evolutionary relationships

monoculture a large stand of a single crop species

monomer a single unit of a multi-unit structure

monophyletic a group that includes an ancestral species and all its descendants

montane growing in a mountainous region

morphology shape and form

motile capable of movement

mucilaginous sticky or gummy

murein a peptidoglycan, a molecule made up of sugar derivatives and amino acids

mutualism a symbiosis between two organisms in which both benefit

mycelium the vegetative body of a fungus, made up of threadlike hyphae

$NADP^+$ oxidized form of nicotinamide adenine dinucleotide phosphate

NADPH reduced form of nicotinamide adenine dinucleotide phosphate, a small, water-soluble molecule that acts as a hydrogen carrier in biochemical reactions

nanometer one billionth of a meter

nectaries organs in flowers that secrete nectar

negative feedback a process by which an increase in some variable causes a response that leads to a decrease in that variable

neuromuscular junction the place on the muscle surface where the muscle receives stimulus from the nervous system

neurotransmitter a chemical that passes messages between nerve cells

node branching site on a stem

nomenclature a naming system

nonmotile not moving

nonpolar not directed along the root-shoot axis, or not marked by separation of charge (unlike water and other polar substances)

nonsecretory not involved in secretion, or the release of materials

Northern Blot a technique for separating RNA molecules by electrophoresis and then identifying a target fragment with a DNA probe

nucleolar related to the nucleolus, a distinct region in the nucleus

nurseryman a worker in a plant nursery

obligate required, without another option

obligate parasite a parasite without a free-living stage in the life cycle

odorant a molecule with an odor

organelle a membrane-bound structure within a cell

osmosis the movement of water across a membrane to a region of high solute concentration

oviposition egg-laying

oxidation reaction with oxygen, or loss of electrons in a chemical reaction

paleobotany the study of ancient plants and plant communities

pangenesis the belief that acquired traits can be inherited by bodily influences on the reproductive cells

panicle a type of inflorescence (flower cluster) that is loosely packed and irregularly branched

paraphyletic group a taxonomic group that excludes one or more descendants of a common ancestor

parenchyma one of three types of cells found in ground tissue

pastoralists farming people who keep animal flocks

pathogen disease-causing organism

pedicel a plant stalk that supports a fruiting or spore-bearing organ

pentamerous composed of five parts

percolate to move through, as a fluid through a solid

peribacteroid a membrane surrounding individual or groups of rhizobia bacteria within the root cells of their host; in such situations the bacteria

have frequently undergone some change in surface chemistry and are referred to as bacteroids

pericycle cell layer between the conducting tissue and the endodermis

permeability the property of being permeable, or open to the passage of other substances

petiole the stalk of a leaf, by which it attaches to the stem

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral. Low pH numbers indicate high acidity while high numbers indicate alkalinity

pharmacognosy the study of drugs derived from natural products

pharmacopeia a group of medicines

phenology seasonal or other time-related aspects of an organism's life

pheromone a chemical released by one organism to influence the behavior of another

photooxidize to react with oxygen under the influence of sunlight

photoperiod the period in which an organism is exposed to light or is sensitive to light exposure, causing flowering or other light-sensitive changes

photoprotectant molecules that protect against damage by sunlight

phylogenetic related to phylogeny, the evolutionary development of a species

physiology the biochemical processes carried out by an organism

phytogeographer a scientist who studies the distribution of plants

pigments colored molecules

pistil the female reproductive organ of a flower

plasmodesmata cell-cell junctions that allow passage of small molecules between cells

polyculture mixed species

polyhedral in the form of a polyhedron, a solid whose sides are polygons

polymer a large molecule made from many similar parts

polynomial "many-named"; a name composed of several individual parts

polyploidy having multiple sets of chromosomes

polysaccharide a linked chain of many sugar molecules

population a group of organisms of a single species that exist in the same region and interbreed

porosity openness

positive feedback a process by which an increase in some variable causes a response that leads to a further increase in that variable

precipitation rainfall; or the process of a substance separating from a solution

pre-Columbian before Columbus

precursor a substance from which another is made

predation the act of preying upon; consuming for food

primordial primitive or early

progenitor parent or ancestor

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

propagate to create more of through sexual or asexual reproduction

protist a usually single-celled organism with a cell nucleus, of the kingdom Protista

protoplasmic related to the protoplasm, cell material within the cell wall

protoplast the portion of a cell within the cell wall

psychoactive causing an effect on the brain

pubescence covered with short hairs

pyruvic acid a three-carbon compound that forms an important intermediate in many cellular processes

quadruple hybrid hybridized plant with four parents

quantitative numerical, especially as derived from measurement

quid a wad for chewing

quinone chemical compound found in plants, often used in making dyes

radii distance across, especially across a circle (singular = radius)

radioisotopes radioactive forms of an element

rambling habit growing without obvious intended direction

reaction center a protein complex that uses light energy to create a stable charge separation by transferring a single electron energetically uphill from a donor molecule to an acceptor molecule, both of which are located in the reaction center

redox oxidation and reduction

regurgitant material brought up from the stomach

Renaissance a period of artistic and intellectual expansion in Europe from the fourteenth to the sixteenth century

salinization increase in salt content

samara a winged seed

saprophytes plants that feed on decaying parts of other plants

saturated containing as much dissolved substance as possible

sclerenchyma one of three cell types in ground tissue

sedimentation deposit of mud, sand, shell, or other material

semidwarf a variety that is intermediate in size between dwarf and full-size varieties

senescent aging or dying

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

sequester to remove from circulation; lock up

serology the study of serum, the liquid, noncellular portion of blood

seta a stiff hair or bristle

silage livestock food produced by fermentation in a silo

siliceous composed of silica, a mineral

silicified composed of silicate minerals

soil horizon distinct layers of soil

solute a substance dissolved in a solution

Southern blot a technique for separating DNA fragments by electrophoresis and then identifying a target fragment with a DNA probe

spasticity abnormal muscle activity caused by damage to the nerve pathways controlling movement

speciation the creation of new species

specimen an object or organism under consideration

speciose marked by many species

sporophyte the diploid, spore-producing individual in the plant life cycle

sporulate to produce or release spores

sterile not capable or involved in reproduction, or unable to support life

sterols chemicals related to steroid hormones

stolons underground stems that may sprout and form new individuals

stomata openings between guard cells on the underside of leaves that allow gas exchange

stratification layering, or separation in space

stratigraphic geology the study of rock layers

stratigraphy the analysis of strata (layered rock)

strobili cone-like reproductive structures

subalpine a region less cold or elevated than alpine (mountaintop)

substrate the physical structure to which an organism attaches, or a molecule acted on by enzymes

succession the pattern of changes in plant species that occurs after a soil disturbance

succulent fleshy, moist

suckers naturally occuring adventitious shoots

suffrutescent a shrub-like plant with a woody base

sulfate a negatively charged particle combining sulfur and oxygen

surfaced smoothed for examination

susceptibility vulnerability

suture line of attachment

swidden agriculture the practice of farming an area until the soil has been depleted and then moving on

symbiont one member of a symbiotic association

symbiosis a relationship between organisms of two different species in which at least one benefits

systematists scientists who study systematics, the classification of species to reflect evolutionary relationships

systemic spread throughout the plant

tannins compounds produced by plants that usually serve protective functions, often colored and used for "tanning" and dyeing

taxa a type of organism, or a level of classification of organisms

tensile forces forces causing tension, or pulling apart; the opposite of compression

tepal an undifferentiated sepal or petal

Tertiary period geologic period from sixty-five to five million years ago

tetraploid having four sets of chromosomes; a form of polyploidy

thallus simple, flattened, nonleafy plant body

tilth soil structure characterized by open air spaces and high water storage capacity due to high levels of organic matter

tonoplast the membrane of the vacuole

topographic related to the shape or contours of the land

totipotent capable of forming entire plants from individual cells

toxin a poisonous substance

tracheid a type of xylem cell that conducts water from root to shoot

transcription factors proteins that bind to a specific DNA sequence called the promoter to regulate the expression of a nearby gene

translocate to move materials from one region to another

translucent allowing the passage of light

transmutation to change from one form to another

transpiration movement of water from soil to atmosphere through a plant

transverse across, or side to side

tribe a group of closely related genera

trophic related to feeding

turgor pressure the outward pressure exerted on the cell wall by the fluid within

twining twisting around while climbing

ultrastructural the level of structure visible with the electron microscope; very small details of structure

uniformitarian the geologic doctrine that formative processes on earth have proceeded at the same rate through time since earth's beginning

uplift raising up of rock layers, a geologic process caused by plate tectonics

urbanization increase in size or number of cities

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Used for storage and maintaining internal pressure

vascular plants plants with specialized transport cells; plants other than bryophytes

vascular related to the transport of nutrients, or related to blood vessels

vector a carrier, usually one that is not affected by the thing carried

vernal related to the spring season

vesicle a membrane-bound cell structure with specialized contents

viable able to live or to function

volatile easily released as a gas

volatilization the release of a gaseous substance

water table the level of water in the soil

whorl a ring

wort an old English term for plant; also an intermediate liquid in beer making

xenobiotics biomolecules from outside the plant, especially molecules that are potentially harmful

xeromorphic a form adapted for dry conditions

xerophytes plants adapted for growth in dry areas

zonation division into zones having different properties

zoospore a swimming spore

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

Topic Outline

ADAPTATIONS

Alkaloids
Allelopathy
Cacti
Cells, Specialized Types
Clines and Ecotypes
Defenses, Chemical
Defenses, Physical
Halophytes
Lichens
Mycorrhizae
Nitrogen Fixation
Poisonous Plants
Seed Dispersal
Shape and Form of Plants
Symbiosis
Translocation
Trichomes

AGRICULTURE

Agriculture, History of
Agriculture, Modern
Agriculture, Organic
Agricultural Ecosystems
Agronomist
Alliaceae
Asteraceae
Biofuels
Borlaug, Norman
Breeder
Breeding
Burbank, Luther
Cacao
Carver, George W.
Coffee
Compost
Cork
Corn
Cotton
Economic Importance of Plants
Ethnobotany
Fertilizer
Fiber and Fiber Products
Food Scientist
Fruits
Fruits, Seedless
Genetic Engineer
Genetic Engineering
Grains
Grasslands
Green Revolution
Halophytes
Herbs and Spices
Herbicides
Horticulture
Horticulturist
Hydroponics
Native Food Crops
Nitrogen Fixation
Oils, Plant-Derived
Pathogens
Pathologist
Polyploidy
Potato
Potato Blight
Quantitative Trait Loci
Rice
Seed Preservation
Soil, Chemistry of
Soil, Physical Characteristics
Solanaceae
Soybeans
Sugar
Tea
Tissue Culture

Tobacco
Transgenic Plants
Vavilov, N. I.
Vegetables
Weeds
Wheat
Wine and Beer Industry

ANATOMY

Anatomy of Plants
Bark
Botanical and Scientific Illustrator
Cell Walls
Cells
Cells, Specialized Types
Cork
Differentiation and Development
Fiber and Fiber Products
Flowers
Fruits
Inflorescence
Leaves
Meristems
Mycorrhizae
Phyllotaxis
Plants
Roots
Seeds
Shape and Form of Plants
Stems
Tissues
Tree Architecture
Trichomes
Vascular Tissues
Vegetables
Wood Anatomy

BIOCHEMISTRY/PHYSIOLOGY

Alcoholic Beverage Industry
Alkaloids
Anthocyanins
Biofuels
Biogeochemical Cycles
Bioremediation
Carbohydrates
Carbon Cycle
Cells
Cellulose
Chlorophyll
Chloroplasts
Cytokinins
Defenses, Chemical
Ecology, Energy Flow
Fertilizer
Flavonoids
Flavor and Fragrance Chemist
Halophytes
Herbicides
Hormones
Lipids
Medicinal Plants
Nitrogen Fixation
Nutrients
Oils, Plant-Derived
Pharmaceutical Scientist
Photoperiodism
Photosynthesis, Carbon Fixation
Photosynthesis, Light Reactions
Physiologist
Pigments
Poisonous Plants
Psychoactive Plants
Soil, Chemistry of
Terpenes
Translocation
Vacuoles
Water Movement

BIODIVERSITY

Agricultural Ecosystems
Aquatic Ecosystems
Biodiversity
Biogeography
Biome
Botanical Gardens and Arboreta
Chapparal
Clines and Ecotypes
Coastal Ecosystems
Coniferous Forests
Curator of a Botanical Garden
Curator of an Herbarium
Deciduous Forests
Deforestation
Desertification
Deserts
Ecology
Ethnobotany
Global Warming
Herbaria
Human Impacts
Invasive Species

Plant Prospecting
Rain Forest Canopy
Rain Forests
Savanna
Taxonomist
Tundra
Wetlands

BIOMES

Aquatic Ecosystems
Atmosphere and Plants
Biodiversity
Biogeography
Biome
Cacti
Chapparal
Coastal Ecosystems
Coniferous Forests
Deciduous Forests
Deforestation
Desertification
Deserts
Ecology
Ecosystem
Global Warning
Grasslands
Human Impacts
Invasive Species
Peat Bogs
Plant Prospecting
Rain Forest Canopy
Rain Forests
Savanna
Tundra
Wetlands

CAREERS

Agriculture, Modern
Agriculture, Organic
Agronomist
Alcoholic Beverage Industry
Arborist
Botanical and Scientific Illustrator
Breeder
Breeding
College Professor
Curator of a Botanical Garden
Curator of an Herbarium
Flavor and Fragrance Chemist
Food Scientist
Forester
Forestry
Genetic Engineer
Genetic Engineering
Horticulture
Horticulturist
Landscape Architect
Pathologist
Pharmaceutical Scientist
Physiologist
Plant Prospecting
Taxonomist
Turf Management

CELL BIOLOGY

Algae
Biogeochemical Cycles
Cell Cycle
Cell Walls
Cells
Cells, Specialized Types
Cellulose
Chloroplasts
Cork
Differentiation and Development
Embryogenesis
Fiber and Fiber Products
Germination
Germination and Growth
Leaves
Meristems
Molecular Plant Genetics
Mycorrhizae
Nitrogen Fixation
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Reproduction, Fertilization
Roots
Seeds
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Tissues
Translocation
Trichomes
Tropisms and Nastic Movements
Vacuoles
Vascular Tissues
Water Movement
Wood Anatomy

DESERTS

Biome
Cacti

Desertification
Deserts
Ecosystem
Halophytes
Native Food Crops
Photosynthesis, Carbon Fixation and
Tundra

DISEASES OF PLANTS

Acid Rain
Chestnut Blight
Deforestation
Dutch Elm Disease
Fungi
Interactions, Plant-Fungal
Interactions, Plant-Insect
Nutrients
Pathogens
Pathologist
Potato Blight

DRUGS AND POISONS

Alcoholic Beverage Industry
Alcoholic Beverages
Alkaloids
Cacao
Cannabis
Coca
Coffee
Defenses, Chemical
Dioscorea
Economic Importance of Plants
Ethnobotany
Flavonoids
Medicinal Plants
Pharmaceutical Scientist
Plant Prospecting
Poison Ivy
Poisonous Plants
Psychoactive Plants
Solanaceae
Tea
Tobacco

ECOLOGY

Acid Rain
Agricultural Ecosystems
Aquatic Ecosystems
Atmosphere and Plants
Biodiversity
Biogeochemical Cycles
Biogeography
Biome
Carbon Cycle
Chapparal
Clines and Ecotypes
Coastal Ecosystems
Coniferous Forests
Deciduous Forests
Decomposers
Defenses, Chemical
Defenses, Physical
Deforestation
Desertification
Deserts
Ecology
Ecology, Energy Flow
Ecology, Fire
Ecosystem
Endangered Species
Global Warning
Grasslands
Human Impacts
Interactions, Plant-Fungal
Interactions, Plant-Insect
Interactions, Plant-Plant
Interactions, Plant-Vertebrate
Invasive Species
Mycorrhizae
Nutrients
Pathogens
Peat Bogs
Pollination Biology
Rain Forest Canopy
Rain Forests
Savanna
Seed Dispersal
Shape and Form of Plants
Soil, Chemistry of
Soil, Physical Characteristics
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ECONOMIC IMPORTANCE OF PLANTS

Acid Rain
Agricultural Ecosystems
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Agriculture, Modern
Agriculture, Organic

Alcoholic Beverage Industry
Alcoholic Beverages
Bamboo
Biofuels
Bioremediation
Breeder
Cacao
Cannabis
Chestnut Blight
Coffee
Coniferous Forests
Cork
Corn
Cotton
Deciduous Forests
Deforestation
Economic Importance of Plants
Fiber and Fiber Products
Flavor and Fragrance Chemist
Fruits
Fruits, Seedless
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plant sciences

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VOLUME 4

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Preface

Someone once said that if you want to find an alien life form, just go into your backyard and grab the first green thing you see. Although plants evolved on Earth along with the rest of us, they really are about as different and strange and wonderful a group of creatures as one is likely to find anywhere in the universe.

The World of Plants

Consider for a minute just how different plants are. They have no mouths, no eyes or ears, no brain, no muscles. They stand still for their entire lives, planted in the soil like enormous drinking straws wicking gallon after gallon of water from the earth to the atmosphere. Plants live on little more than water, air, and sunshine and have mastered the trick of transmuting these simple things into almost everything they (and we) need. In this encyclopedia, readers will find out how plants accomplish this photosynthetic alchemy and learn about the extraordinary variety of form and function within the plant kingdom. In addition, readers will be able to trace their 450-million-year history and diversification, from the very first primitive land plants to the more than 250,000 species living today.

*Explore further in Photosynthesis, Light Reactions and Evolution of Plants

All animals ultimately depend on photosynthesis for their food, and humans are no exception. Over the past ten thousand years, we have cultivated such an intimate relationship with a few species of grains that it is hardly an exaggeration to say, in the words of one scientist, that "humans domesticated wheat, and vice versa." With the help of agriculture, humans were transformed from a nomadic, hunting and gathering species numbering in the low millions, into the most dominant species on the planet, with a population that currently exceeds six billion. Agriculture has shaped human culture profoundly, and together the two have reshaped the planet. In this encyclopedia, readers can explore the history of agriculture, learn how it is practiced today, both conventionally and organically, and what the impact of it and other human activities has been on the land, the atmosphere, and the other creatures who share the planet with us.

*Explore further in Agriculture, Modern and Human Impacts

Throughout history—even before the development of the modern scientific method—humans experimented with plants, finding the ones that provided the best meal, the strongest fiber, or the sweetest wine. Naming a thing is such a basic and powerful way of knowing it that all cultures have created some type of taxonomy for the plants they use. The scientific understanding of plants through experimentation, and the development of ra-

tional classification schemes based on evolution, has a rich history that is explored in detail in this encyclopedia. There are biographies of more than two dozen botanists who shaped our modern understanding, and essays on the history of physiology, ecology, taxonomy, and evolution. Across the spectrum of the botanical sciences, progress has accelerated in the last two decades, and a range of entries describe the still-changing understanding of evolutionary relationships, genetic control, and biodiversity.

✶Explore further in Ecology, History of; Biodiversity; and Phylogeny

With the development of our modern scientific society, a wide range of new careers has opened up for people interested in plant sciences, many of which are described in this encyclopedia. Most of these jobs require a college degree, and the better-paying ones often require advanced training. While all are centered around plants, they draw on skills that range from envisioning a landscape in one's imagination (landscape architect) to solving differential equations (an ecological modeler) to budgeting and personnel management (curator of a botanical garden).

✶Explore further in Curator of a Botanical Garden and Landscape Architect

Organization of the Material

Each of the 280 entries in *Plant Sciences* has been newly commissioned for this work. Our contributors are drawn from academic and research institutions, industry, and nonprofit organizations throughout North America. In many cases, the authors literally "wrote the book" on their subject, and all have brought their expertise to bear in writing authoritative, up-to-date entries that are nonetheless accessible to high school students. Almost every entry is illustrated and there are numerous photos, tables, boxes, and sidebars to enhance understanding. Unfamiliar terms are highlighted and defined in the margin. Most entries are followed by a list of related articles and a short reading list for readers seeking more information. Front and back matter include a geologic timescale, a topic outline that groups entries thematically, and a glossary. Each volume has its own index, and volume 4 contains a cumulative index covering the entire encyclopedia.

Acknowledgments and Thanks

I wish to thank the many people at Macmillan Reference USA and the Gale Group for their leadership in bringing this work to fruition, and their assiduous attention to the many details that make such a work possible. In particular, thanks to Hélène Potter, Brian Kinsey, Betz Des Chenes, and Diane Sawinski. The editorial board members—Robert Evans, Wendy Mechaber, and Robert Wallace—were outstanding, providing invaluable expertise and extraordinary hard work. Wendy is also my wife, and I wish to thank her for her support and encouragement throughout this project. My own love of plants began with three outstanding biology teachers, Marjorie Holland, James Howell, and Walt Tulecke, and I am in their debt. My many students at the Commonwealth School in Boston were also great teachers—their enthusiastic questions over the years deepened my own understanding and appreciation of the mysteries of the plant world. I hope that a new generation of students can discover some of the excitement and mystery of this world in *Plant Sciences*.

Richard Robinson
Editor in Chief

Geologic Timescale

Era	Period		Epoch	started (millions of years ago)
Cenozoic 66.4 millions of years ago–present time	**Quaternary**		Holocene	0.01
			Pleistocene	1.6
	Tertiary	**Neogene**	Pliocene	5.3
			Miocene	23.7
		Paleogene	Oligocene	36.6
			Eocene	57.8
			Paleocene	66.4
Mesozoic 245–66.4 millions of years ago	**Cretaceous**		Late	97.5
			Early	144
	Jurassic		Late	163
			Middle	187
			Early	208
	Triassic		Late	230
			Middle	240
			Early	245
Paleozoic 570–245 millions of years ago	**Permian**		Late	258
			Early	286
	Carboniferous	**Pennsylvanian**	Late	320
		Mississippian	Early	360
	Devonian		Late	374
			Middle	387
			Early	408
	Silurian		Late	421
			Early	438
	Ordovician		Late	458
			Middle	478
			Early	505
	Cambrian		Late	523
			Middle	540
			Early	570
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Rain Forest Canopy

The rain forest canopy consists of the treetop region or, more precisely, of the aggregate of every tree crown in the rain forest, including foliage, twigs, fine branches, and **epiphytes**. The upper canopy represents the interface between the uppermost layer of leaves and the atmosphere, and, for practical purposes, many researchers consider this layer to be only a few meters deep. Most of the biological activity in and **biodiversity** within tropical rain forests appears to be concentrated in the upper canopy.

epiphytes plants that grow on other plants

biodiversity degree of variety of life

Many **abiotic** and **biotic** characteristics of the canopy are different from the understory beneath. Its higher illumination levels promote more rapid rates of photosynthesis, which, in turn, promote higher vegetal production, and consequently sustain a more abundant and diverse **community** of animals than in the understory. In a much publicized article in 1983, Terry Erwin termed the canopy of tropical forests "the last biotic frontier," referring to the vast, but poorly studied, richness of organisms, particularly arthropods, resident in the canopy.

abiotic nonliving

biotic involving or related to life

community a group of organisms of different species living in a region

Many regional and global ecological processes depend crucially on the integrity of the rain forest canopy, which possesses features unique to this environment. Hence, canopy science represents a young, but blossoming, discipline in the field of natural sciences.

Significance of the Rain Forest Canopy in Ecological Processes

Canopies of all types, including boreal and tropical forests, play a crucial role in the maintenance of ecological processes, although thus far, the attention of researchers has tended to concentrate on those in the tropics, rather than those in temperate climates.

The forest canopy is the principal site for the interchange of heat, oxygen, water vapor, and carbon dioxide. It has been estimated that most photosynthetic activities in the **biosphere** occur in the canopy. Forest canopies account for almost half of the carbon stored in terrestrial vegetation and fix more carbon per year than any other habitat. **Ecophysiological** studies are therefore crucial to predict the impact of increasing atmospheric concentrations of carbon dioxide in global warming. Thus,

biosphere the region of the Earth in which life exists

ecophysiological related to how an organism's physiology affects its function in an ecosystem

A man climbing into a rain forest canopy in Braulio Carrillo National Park in Costa Rica.

forest canopies both control regional climate and play an important role in regulating global climate.

Rain forest canopies sustain countless species of animals and plants, and the majority of them are undiscovered and potentially unexploited resources. This important reservoir of genetic diversity ensures that vital ecological processes are performed by a variety of species, rather than a few, thus maintaining the integrity of the forest **ecosystem** in case of light disturbance. Adequate pollination and seed dispersal by a variety of organisms ensure the regeneration of the forest, whereas herbivory hastens the return of nutrients to ground level and their recycling; all three processes are prevalent in the canopy.

ecosystem an ecological community together with its environment

Unique Features of the Rain Forest Canopy

The uppermost canopy leaves are typically thicker, more upright, and have higher specific leaf mass and higher photosynthetic rates than understory leaves. In closed tropical forests, the upper canopy is more akin to chaparral shrub vegetation than to rain forest understory vegetation. Leaf area density and the abundance of young leaves, flowers, and seeds are also higher in the canopy than in the understory. Microclimatic conditions differ markedly between the canopy and the understory; illumination, air temperature, wind, fluctuation of relative humidity, and water condensation at night are appreciably higher in the former.

Further, the array of tree crowns in the canopy are rather heterogeneous, including different species, size, **phenologies** (e.g., flowering and leaf flushing), and age state. Thus, forest canopies are best considered as spatially complex, three-dimensional structures that are temporally dynamic. Such systems are particularly conductive to the **stratification**, niche differentiation, and habitat selection of canopy organisms.

phenology seasonal or other time-related aspects of an organism's life

stratification layering, or separation in space

Indeed, the rain forest canopy may represent one of the most biodiverse **biotas**, perhaps containing between 50 and 80 percent of terrestrial species, depending on estimates. Besides the support trees, not only are many epiphytic plants (such as lianas, ferns, and orchids), arboreal mammals and reptiles, birds, and bats encountered, but unrivaled numbers of species of insects, spiders, mites, and other arthropods are also present. Ants represent the most regularly abundant animal group in the canopy, both in terms of numbers and **biomass**, whereas the most species-rich groups appear to be rove beetles (Staphylinidae) and weevils (Curculionidae). Typically, arthropod abundance and diversity are between two and four times higher in the canopy than in the understory.

biota the sum total of living organisms in a region of a given size

biomass the total dry weight of an organism or group of organisms

Many of these organisms show distinct physical or behavioral adaptations to arboreal life. These include the canopy root system of several tree species that tap into the **humus** accumulated within epiphytes; the **coalescing roots** of strangling figs; the prehensile tails and gliding membranes of various arboreal mammals; the foraging behavior of particular bird species visiting epiphytes to search for various food resources; or the many peculiar life cycles and specializations (e.g., symbiotic associations) of a multitude of arthropod species. In particular, it is probable that herbivorous insects in the canopy are more host-specific to their host plants than their counterparts in the understory. Interactions between canopy organisms are often complex, due to heterogeneous **substrates** and patchy food resources, often resulting in intriguing **mutualisms**, such as ant gardens, in which ants harvest leaves to feed to cultures of fungi maintained by the colony. However, very little is known of most canopy organisms and their interactions with the canopy environment.

humus the organic material in soil, formed from decaying organisms

coalescing roots roots that grow together

substrate the physical structure to which an organism attaches

mutualism a symbiosis between two organisms in which both benefit

Canopy Access

The means for gaining access to the canopy, a major impediment to canopy science, was developed in the tropics. A pioneering attempt to study the canopy in situ by means of ladders and pulley systems was utilized during Oxford University's expedition of 1929 in Guyana, led by Major R. W. G. Hingston. The few studies performed before the late 1970s used fixed systems such as various towers, platforms, walkways, and ladders. In 1978, Donald Perry reported the inexpensive adaptation of a single-rope technique (used by cave explorers to ascend vertical shafts) to the safe climbing of tall forest trees. This led to an expansion of canopy studies, augmented in the following decade with newer methods permitting access to the upper canopy, including the canopy raft (and accompanying sledge) and canopy cranes. In addition, **entomologists** collect large quantities of canopy arthropods by insecticide knockdown or by hoisting various designs of traps into the canopy. Landscape ecologists also study the canopy with satellite remote sensing. By December 1999, the canopy raft had completed four successful missions, and four canopy cranes were in continuous use in the tropics. The scientific exploration and study of one of the most significant, exciting, and endangered habitats on Earth has only just begun. SEE ALSO PLANT PROSPECTING; RAIN FORESTS.

entomologist a scientist who studies insects

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Rain Forests

Since rainfall controls tropical vegetation in the tropics, rain forest types may be classified with reference to local climate. These include lowland, **montane**, subtropical, and temperate rain forests. Their common features are at least 1,500 millimeters (approximately 33 inches) of annual rainfall and evergreen vegetation with lianas and **epiphytes**. Most widespread are lowland tropical rain forests, accounting for less than one-third of the tropical land surface, growing in areas receiving between 2,000 to 5,000 millimeters of annual rainfall, with relatively high and constant air temperature (annual mean ± 25°C) never below freezing point. They persist in Central America, the Amazon Basin, the Congo Basin, Southeast Asia, New Guinea, and northern Australia. Their canopy is often 25 to 45 meters or higher.

montane growing in a mountainous region

epiphytes plants that grow on other plants

In the monsoonal tropics, characterized by similar total annual rainfall, but unevenly distributed between dry and wet seasons, a related type of low-

Lush tropical rain forest vegetation on Atiu Island in the Cook Islands.

land forest is found, which becomes partly leafless during the driest months. These tropical evergreen seasonal forests occur in Central America, the northern coast of South America, Africa, India, Southeast Asia, and in some of the Pacific Islands.

Montane tropical rain forests grow in the same regions that lowland forests do, but at higher altitudes, often above 1,000 meters. Local climate is cooler (15 to 25°C), with high annual rainfall (2,000 to 4,000 millimeters or more). The canopy is often 15 to 35 meters in lower montane forest, while above 2,000 meters, in upper montane forests, it is only 10 meters or less. Fog is frequent, and in moss forests relative humidity varies little from saturation point.

Subtropical rain forests are found in the southeastern United States, southwestern South America, southern China, Japan, eastern Australia, and New Zealand, often within cooler climates (15 to 20°C) and lower rainfall (1,500 to 2,000 millimeters). The canopy generally ranges between 35 and 40 meters. Temperate rain forests occur mostly along the Pacific Coast of North America (where the canopy may be 60 meters or higher), Tasmania, and New Zealand. Although temperatures often fall below freezing point, annual rainfall remains high. In addition, wetland forests include mangrove forests, occurring in saline coastal waters, and various peat and freshwater swamp forests. The rest of this overview concentrates on tropical lowland rain forests.

Rain Forest Structure

Rain forest structure is highly complex and determined by competition for light among plant species. Isolated trees, emerging above the canopy, are often present and can be 70 to 80 meters in height. Different tree species grow following various architectural models related to bud location and branching patterns and may or may not form distinct forest layers. Lianas rooted in the ground and epiphytes (e.g., ferns, orchids, and bromeliads) growing on support branches are common in the canopy. Leaves are often medium to large in size, lustrous, and tough. Their shape is often simple, ending with a "drip tip" to shed rainfall. Compound leaves are thought to represent an adaptation to rapid upward growth or seasonal drought and occur more commonly among plants growing in light gaps, in early successional vegetation, or in tropical evergreen seasonal forests. Very little of the light falling on the canopy reaches the ground (0.5 to 2 percent of the illumination available in the canopy), so that the herb layer is much reduced but also includes some **saprophytes** and root-parasites. Although larger herbs from *Zingiberales* and *Arales* may occasionally form denser understory, in mature rain forests it is usually not difficult to penetrate.

saprophytes plants that feed on decaying parts of other plants

This structural complexity is complicated by the temporal dynamics of the rain forest. Often, leaf fall occurs during the driest months and leaf flushing (budding and growth) during the wettest. Furthermore, rain forest trees show a variety of leafing **phenologies**, from continuous leafing, intermittent flushing to deciduous habits. Within the same species or individual crown, flushing may be synchronous or not. Patterns of flowering and fruiting are equally complex, with sometimes mass flowering or fruiting. Understory leaves are often long-lived, more than five years, and covered with mats of epiphytes (such as mosses, lichens, and algae).

phenology seasonal or other time-related aspects of an organism's life

Plant Diversity in Rain Forests

Several theories account for the higher plant and animal diversity in tropical forests compared to temperate forests. First, a greater stability may have existed in the tropics, in comparison with temperate lands, where **biotas** have been depleted by recent glaciations. During the Pleistocene epoch, ten thousand years ago, climatic changes transformed many rain forests into drier savanna. Some rain forests persisted as refugia (isolated refuges), later rejoining together as the climate became more favorable, increasing species richness within. Second, tropical **ecosystems** may provide more ecological niches than temperate ones, thereby supporting more species. Third, **predation** and competition in the tropics may promote higher speciation rates. Last, high species richness in the tropics may result from solar energy controlling **biodiversity** in near-saturated humid conditions.

biota the sum total of living organisms in a region of a given size

ecosystem an ecological community together with its environment

predation the act of preying upon; consuming for food

biodiversity degree of variety of life

genera plural of genus

The great majority of plants in rain forests consist of dicotyledonous trees. For example, the **genera** *Ficus* (Moraceae) and *Piper* (Piperaceae) are diverse throughout the tropics, whereas *Eperua* (Caesalpiniaceae) and *Shorea* (Dipterocarpaceae) are species-rich in Neotropical and Asian forests, respectively. Some families that are herbaceous in temperate areas develop as woody trees in rain forests (e.g., Verbenaceae, Urticaceae, and Polygalaceae). Monocotyledons are less common but include palm trees, various herbs, orchids, and grasses. Abundant woody climbers (often dicotyledons) are characteristic of rain forest vegetation. Their broad stems may cover several kilo-

Epiphytes cover trees in an Ecuadoran rain forest.

meters of canopy. Herbaceous or shrubby epiphytes, semiparasitic mistletoes, and strangling figs (*Ficus*) are also species-rich.

Although tropical rain forests cover less than 6 percent of land masses, they may sustain half or more of Earth's biodiversity. For example, the Malay Peninsula contains about 7,900 plant species compared to Britain's 1,430. Further, a typical hectare of rain forest may include 150 to 200 species of trees with a diameter greater than 10 centimeters, with records of 300 species per hectare in Peruvian Amazonia. In contrast, a hectare of temperate deciduous forest might contain only one-tenth as many species. Still, many rain forest tree species are rare, with average densities of 0.3 to 0.6 trees per species and per hectare. This results in a large average distance between trees of the same species that may affect pollinating and foraging animals, as well as the plants themselves. Indeed, pests or diseases are rarely a problem in mixed rain forests, while uniform vegetation in the same area, such as plantations, is often heavily defoliated.

Contrasting strongly with mixed rain forests, monodominant rain forests are dominated by a single canopy species, such as *Mora* (Caesalpiniaceae) in the Neotropical region, *Gilbertiodendron* (Caesalpiniaceae) in Africa, and *Dryobalanops* (Dipterocarpacea) or *Nothofagus* (Fagaceae) in Australasia. These are competitively superior, shade-tolerant, slow-growing, long-lived species with large and poorly dispersed seeds.

Animal Diversity in Rain Forests

Rain forests sustain more faunal diversity than any other habitat on Earth. In particular, the Amazonian forests of Peru and Ecuador are the most diverse for mammals, birds, reptiles, amphibians, and butterflies. Arthropods are particularly diverse in rain forests since they exploit every niche from the soil to the canopy. For example, one large tree in Peru yielded 43 species of ants, equivalent to their entire British fauna, and 134 species of leaf beetles (Chrysomelidae) were collected from ten tree species in New Guinea in comparison with a total fauna of 255 British species.

The most abundant vertebrates in rain forests are frugivores, feeding on fruits and seeds. Among invertebrates (aside from earthworms in soil and epiphytes), the dominant groups rely on a variety of food ressources. These include ants (Formicidae: predators, **herbivores**, or fungal-feeders), rove beetles (Staphylinidae: predators, scavengers, or fungal-feeders) or weevils (Curculionidae: leaf-chewers, wood-, seed-, or flower-eaters). Other important invertebrate groups in rain forests include parasitoid wasps, moths, leaf beetles, and spiders. However, most of these species are little known and many are yet to be described.

herbivore an organism that feeds on plant parts

In 1982, **entomologist** Terry Erwin suggested that there may be as many as 30 million species of arthropods, instead of the previously estimated 1.5 million, although this has not been substantiated. Erwin's estimates attracted considerable attention to the vast, but endangered, reservoir of genetic diversity represented by rain forest arthropods. In 1988, Erwin stated "no matter what the number we are talking about, whether 1 million or 20 million [arthropod species], it is massive destruction of the biological richness of Earth."

entomologist a scientist who studies insects

Rain Forest Dynamics: Regeneration

Rain forest regeneration and continuity is assured through the important processes of pollination and seed dispersal, which occur primarily through the movements of rain forest animals. Their loss in severely disturbed rain forests drastically affects regeneration capacity. Wind pollination, common in temperate regions, is rarer due to the absence of wind currents; 90 percent of rain forest plants may be insect-pollinated, with nectar the reward for pollinators. They may be strong fliers that forage over long distances, such as birds, bats, hawk moths, and large **euglossine bees**, which may fly up to 23 kilometers. Other short-range pollinators may include stingless, carpenter, and bumblebees, wasps, butterflies, thrips, beetles, midges, and flies. Depending on the timing of flower opening, pollinators may be either **diurnal** or nocturnal.

euglossine bees a group of bees that pollinate orchids and other rainforest plants

diurnal daily, or by day

Another important aspect of pollination is fidelity to particular plant species, which ensures cross-pollination. Some pollinators are generalists (e.g., stingless bees) but restrict their visits to particular plant species. However, many rain forest plants have developed intricate relationships with their pollinators. For example, the petal tube of many flowers corresponds exactly in length and curvature to either the beaks of hummingbirds or to the tongue of certain hawk moths. Further, pollinator activities are attuned to different flowering phenologies, the most specialized of these involving figs (*Ficus*) and fig wasps (Agaonidae), the former totally dependent on the latter for pollination. Usually, one particular species of fig is pollinated only by its own species of wasp.

Some rain forest plants may be dispersed by wind or gravity. However, many of them rely on animals such as ants, fish, reptiles, birds, bats, primates, deer, pigs, civets, rodents, and elephants to disperse seeds. This ensures pollination and cross-fertilization of distant tree **populations** to produce more vigorous and successful offspring and that seedlings have enough space and light to grow and develop. Fruits represent fleshy rewards for animals; swallowed with their seeds, the latter emerge intact in feces and ready to germinate. Animals often specialize in particular seeds or similar seed

population a group of organisms of a single species that exist in the same region and interbreed

Leaf-cutter ants carry their quarry in a Peruvian rain forest.

types, with larger animals often dispersing the seeds at great distance from the parent tree.

Figs are a year-round resource for rain forest frugivores and are particularly important when other fruits become scare. Fig trees are referred to as a keystone species, those that have a crucial importance in the maintenance of the rain forest ecosystem.

Insects (e.g., Bruchidae and Curculionidae), parrots, or squirrels may overcome the chemical defenses of seeds, feeding on them without dispersal. Many insects and fungi also attack the leaves and stems of seedlings. Patterns of herbivore attack below the parent trees may depend on seedling density and decrease with increasing distance from the parent. This may result from specific insect herbivores colonizing seedlings from parent trees, promoting botanical diversity by prohibiting the establishment of young trees near conspecific parents. However, this is not universal, and this model requires validation and refinement.

Rain Forest Dynamics: Succession

Natural disturbance induces a succession of vegetation. After clearance, rain forest succession may start with almost bare soil, proceed with a different kind of vegetation (called secondary forest or growth), and end with the restoration of the original, climax, vegetation. For example, the fall of a large crown of 20 meters in diameter may produce a forest gap of 400 m^2. Some plants will be damaged from the tree fall, but others will have improved growth opportunities, due to increased access to light. Forest gaps are common and promote local plant and animal diversity.

Secondary rain forests contain smaller trees, with many small climbers and young saplings in an understory that is often difficult to penetrate. The floral composition of these forests is different from primary rain forests. Although a few secondary species may live in natural gaps created by treefalls in primary forests, they are more abundant in secondary forests. These are dominated by a few plant species and are less species rich than primary forests. Secondary genera include *Cecropia* (Cecropiaceae) in the Neotropical region, *Musanga* (Moraceae) in Africa, and *Macaranga* (Euphorbiaceae) in Asia. Typically, these "pioneer species" (as opposed to the shade-tolerant species of primary rain forests) produce large quantities of small seeds carried by wind or small animals. In contrast, shade-tolerant species often bear large seeds in fleshy fruits that are dispersed by large animals. Pioneers germinate and grow rapidly (often several meters in two to three years), producing thin, short-lived, and large leaves on weak stems that break easily. Secondary vegetation is not long-lived, since species needing much sunlight to germinate and grow eventually die in the shade of their parents. These stands of pioneers are unable to regenerate under new ecological conditions, giving way to slower-growing, stronger trees that regenerate primary forest, a process that takes place over many centuries.

Herbivory and Decomposition in Rain Forests

Both herbivory and decomposition hasten the return and recycling of nutrients in the ground and promote regeneration of the forest. Most rain forest plants contain more chemical defenses than temperate plants. This may be a response to year-round high herbivore pressure, particularly from insects that represent the bulk of leaf-eating, sap-sucking, flower- and seed-eating fauna. Chemical defenses are often by-products of plant metabolism and are termed secondary metabolites, including lectins, resins, **alkaloids**, protease inhibitors, **cyanogenic** glycosides, or rare amino acids. Each plant species may contain fifty or more in its leaves, bark, or seeds. Many may be pharmacologically active, with subtle differences often due to the high genetic variation of rain forest plants. Since 99 percent of rain forest plants have not been yet chemically screened, biological prospecting for secondary metabolites was undervalued until recently—with an even greater percentage of arthropods untreated.

alkaloids bitter secondary plant compounds, often used for defense

cyanogenic giving rise to cyanide

Herbivorous insects have developed assorted strategies to counter the plants' chemical defenses and concentrate their damage on young leaves. They may produce **enzymes** capable of breaking down secondary metabolites, thus becoming restricted to feeding on one or a few related plant species sharing similar chemical properties. About 9 percent of leaf area is usually lost to herbivores in tropical rain forests, a figure often considerably lower in forests growing on nutrient-poor soils. Since they invest most of their energy in growth and less in chemical defenses, herbivory on pioneer trees tends to be greater than those that are shade tolerant.

enzyme a protein that controls a reaction in a cell

Decomposition of organic matter, performed by fungi, bacteria, and invertebrates, particularly earthworms, is rapid in rain forests. Termites are the primary decomposers of wood, often transporting rotting wood to great depths in their underground galleries. In terms of dominance, termites are ranked second to ants with up to 870 colonies per hectare, including underground and arboreal nests.

Nutrient Cycling in Rain Forests and the Consequences of Deforestation

Although most tropical rain forests grow on nutrient-poor soils, their primary production is the highest of any natural system, ranging from 300 to 900 tons of **biomass** per hectare. This is due to the efficient cycling of

biomass the total dry weight of an organism or group of organisms

nutrients through a virtually leak-proof system, since up to 90 percent of nutrients may be stored at anytime in the vegetation.

The main source of nutrients is rainfall, which represents as much as 3 kilograms of phosphorus, 2 kilograms of iron, and 10 kilograms of nitrogen per hectare per year. The forest filters out nutrients from the water as it passes through. Epiphytes growing on leaf surfaces often fix nitrogen. At ground level, tree roots, which may extend near the soil surface 100 meters away from the tree trunks, may be three times as dense as in temperate forests and are very efficient at absorbing nutrients from the soil, whether from rainfall or from decaying organic matter. Symbiotic associations between roots and fungus or bacteria (termed mycorrhizae) are particularly efficient in recovering minerals, particularly phosphorus, from leaf litter.

Since most nutrients are held in the vegetation aboveground, clearing and burning of rain forests concentrates nutrients in the ground. Some nitrogen and sulfur are lost during burning, but large quantities of other nutrients are deposited in ash. Leaching, due to heavy rainfall, washes these nutrients far beyond the shorter roots of new grasses or shrubs. This severely disrupts the nutrient cycle, leaving barren tracts that remain unproductive or that require the ecologically unsound overapplication of fertilizers. Moreover, the clearing and removal of logs by heavy machinery result in soil **compaction**, water runoff, and, eventually, soil erosion. When a large area of forest is cleared, the soil becomes drier and warmer, and most of the mycorrhizae die out. Aided by nutrients, mycorrhizae, and seeds from nearby intact rain forest patches, regrowth occurs in small areas of clearance, but this is impossible for large clearings, where herbaceous vegetation **colonizes** infertile soils.

compaction compacting of soil, leading to loss of air spaces

colonize to inhabit a new area

Indigenous People and Rain Forests

The indigenous dwellers of rain forests are dependent on them and, similarly, are endangered by habitat fragmentation and destruction. This includes several groups in Malaysia (the Orang Asli), Sarawak (the Penan), Sabah, New Guinea, the Philippines, the African Pygmy groups in Cameroon, Gabon, and Congo; and many Amerindian groups, such as the Yanomami of Brazil or Jívaro of Ecuador.

The encyclopedic knowledge of the natural world of many indigenous groups is well known and discussed by many rain forest ecologists. For example, Papua New Guineans know hundreds of plant and animal species living in their forests, and they have developed detailed **nomenclatural** systems in their local languages. This knowledge is not restricted to medicinal plants but also extends to the smallest of creatures. Indigenous knowledge is an inspiration for scientific research and an opportunity for inclusion of local assistants within research projects. Such knowledge also requires reward through the sharing of profits that may result from economically important discoveries.

nomenclatural related to naming or naming conventions

Environmental Threats to Rain Forests

The major threats to rain forests are, in order of decreasing importance:

1. cattle ranching and farming, leading to habitat fragmentation and destruction

cultivation growth of crop plants, or turning the soil for this purpose

2. clear-cutting for timber and pulp, with similar outcomes
3. plantation **cultivation**, creating large areas of secondary regrowth
4. selective logging of particular tree species, leading to an irregularly structured patchwork of primary and secondary forests
5. shifting cultivation (slash-and-burn), creating small patches of secondary growth
6. natural disasters, including localized landslides and fires, leading to secondary regrowth and natural succession.

The ever-increasing and often irreversible human damage to rain forests shows no sign of slowing down. Although much controversy exists regarding rates of its loss (perhaps 50 hectares per minute) and biodiversity, it is probable that, in a few decades, large tracts of rain forests will remain only in the Guianas, upper Amazon, Congo Basin, and New Guinea. Tragically, a substantial part of Earth's biodiversity and genetic resources will be lost forever, with the potential for concomitantly disastrous effects on local and global climates. Belief that recent advances in biotechnology will remedy this situation is erroneous. The best way to slow down these alarming rates of loss is through education, conservation, and rehabilitation of the organismic components of ecology, botany, zoology, and taxonomy. SEE ALSO Biodiversity; Defenses, Chemical; Deforestation; Endangered Species; Plant Prospecting; Pollination; Rain Forest Canopy; Seed Dispersal.

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Record-Holding Plants

Of all the kingdoms of living organisms, the plant kingdom exhibits the greatest extremes of size and scale of individuals. From gigantic, massive organisms to extremely small ones, the plant species truly demonstrate the immense range of growth forms and size differences. Some record-holding plants are listed in this article; however, additional research may disclose new records of interest to botanists.

Largest Plant. An individual plant of giant sequoia (*Sequoiadendron giganteum*) in Sequoia National Park, California, named the "General Sherman Tree" is considered to be the largest living plant, as well as the largest living thing on Earth. It is a cone-bearing **gymnosperm** with a height of 84 meters (275 feet) and a measured trunk girth of 31.3 meters (102.6 feet). This plant has enough wood in its trunk to supply the lumber to build about forty small houses.

gymnosperm a major group of plants that includes the conifers

Largest Leaves. Two related plants compete for the title of the largest-leaved plant: the raffia palm (*Raphia farinifera*) of the Mascarene Islands and the bamboo palm (*Raphia taedigera*) of the Amazon basin in South America both have leaves of similar, gigantic size. The blades of their leaves have been measured to be 20 meters (65.2 feet) and their **petioles** measured approximately 4 meters (13 feet). Their total leaf length (24 meters; 78 feet) is equivalent to the height of a seven-story building.

petiole the stalk of a leaf, by which it attaches to the stem

Longest Total Root Length. A plant of the grass known as rye (*Secale cereale*), which has an extensive fibrous root system, was shown to have a total root length of 623 kilometers (387 miles).

A specimen of *Puya raymondii,* which holds the record for the world's largest inflorescence, grows at the foot of mountains in Peru's Huascaran National Park.

Deepest Roots. A species of fig (*Ficus*, family Moraceae) from the Transvaal of South Africa was determined to have roots reaching at least 122 meters (400 feet).

inflorescence an arrangement of flowers on a stalk

panicle type of inflorescence (flower cluster) that is loosely packed and irregularly branched

Largest Inflorescence. The **inflorescence** of *Puya raimondii*, a rosette-leaved member of the pineapple family (Bromeliaceae), is produced after 80 to 150 years of nonreproductive growth. It develops a **panicle** of over 10 meters (35 feet) in height, and produces up to eight thousand white flowers. After flowering and producing thousands of fruit on its gigantic inflorescence, the plant dies.

Largest Flower. A vining tropical plant from the jungles of Southeast Asia, *Rafflesia arnoldii*, known as the corpse lily, has individual flowers that weigh up to 15 kilograms (33 pounds) and diameters reaching 1 meter (39 inches) across. The flowers are pollinated by flies and beetles.

Smallest Plant. The world's smallest flowering plant is a member of the duckweed family (Lemnaceae), *Wolffia angusta*, which is found in Australia. This extremely diminutive aquatic plant measures only 0.61 millimeters (0.024 inches) long and 0.33 millimeters (0.013 inches) wide, and consists of one or two leaves and a very tiny root. The plant floats on the surface of fresh water lakes and ponds and rivers. It flowers annually and produces a very tiny fruit.

Oldest Living Plant. A single individual plant, the creosote bush, in Southern California (*Larrea tridentata* of the sunflower family [Asteraceae]), is estimated to be 11,700 years old.

Oldest Recorded Tree. A coast redwood (*Sequoia sempervirens*), the Eon Tree of Humboldt County, California, fell in December 1977, and was estimated to be more than 6,200 years old. The oldest living tree is a bristlecone pine, *Pinus longaeva*, found in the White Mountains of California. It has been documented to be at least 4,700 years old (measured in 1974).

Largest Tree (Biomass). A giant sequoia (*Sequoiadendron giganteum*), named the General Sherman Tree, is found in Sequoia National Park, California, and is considered the largest living thing in the world. It is also the largest plant.

Tallest Tree (Height). A plant in the myrtle family (Myrtaceae), *Eucalyptus regnans*, from Watts River, Victoria, Australia, was recorded in 1872 to have measured 132.6 meters (435 feet) tall. The tallest presently living tree is the National Geographic Society tree, a coast redwood (*Sequoia sempervirens*) found in Redwood National Park, California, determined to be 111.4 meters (365.5 feet) in height.

Greatest Tree Girth. One individual tree of the European chestnut (*Castanea sativa*) discovered on the island of Sicily was measured in 1780 and found to be 58 meters (190 feet) in circumference. Since that time, the tree's growth has caused it to divide, and it is now separated into three distinct parts.

Tallest Grass. A bamboo species, *Bambusa arundinacea*, from India was measured with a height of 37 meters (121.5 feet) in 1904.

Largest Cactus. The saguaro (*Carnegiea gigantea*) of the Sonoran Desert in Mexico and Arizona is considered the world's largest (tallest) cactus; one individual plant from southern Arizona was measured at nearly 17.8 meters (58 feet) in height. Another species of related columnar cactus, *Pachycereus weberi*, from the state of Oaxaca, Mexico, is likely the largest cactus by weight. While not as tall as the saguaro, it has many more branches and trunk diameters of more than 2 meters, and its mass can only be estimated to be in the range of 3,600 kilograms (4 tons) or more.

Largest Seed. Seeds of the giant fan palm (*Lodoicea maldivica*) called the double coconut weigh approximately 22 kilograms (44 pounds) and are more than 41 centimeters (16 inches) in their longest dimension. Giant fan palms are found on the Seychelles Islands of the Indian Ocean.

Smallest Seed. The nearly microscopic seeds of epiphytic orchids are dispersed by wind currents (similar to pollen), carrying the seeds from the ripe, opened orchid fruits (capsules) and allowing them to land on suitable locations in trees to establish new plants far from the original mother plant.

Fastest-Growing Plant. Various species of bamboo, members of the grass family (Poaceae), have been recorded as having grown up to 1 meter (3 feet) per day. A record on the island of Scilly, England, from 1978 documented that an individual *Hesperoyucca whipplei* (family Agavaceae) grew 4 meters (12 feet) in 14 days, or about 25 centimeters (10 inches) per day.

Slowest-Growing Tree. Of naturally occurring plants, a cycad (a gymnosperm) *Dioon edule*, has been reported as having the slowest growth rate: 0.76 millimeters (0.03 inches) per year. A plant with an age of 120 years measured only 10 centimeters (4 inches) tall. SEE ALSO DENDROCHRONOLOGY; SEQUOIA; TREES.

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Reproduction, Alternation of Generations and

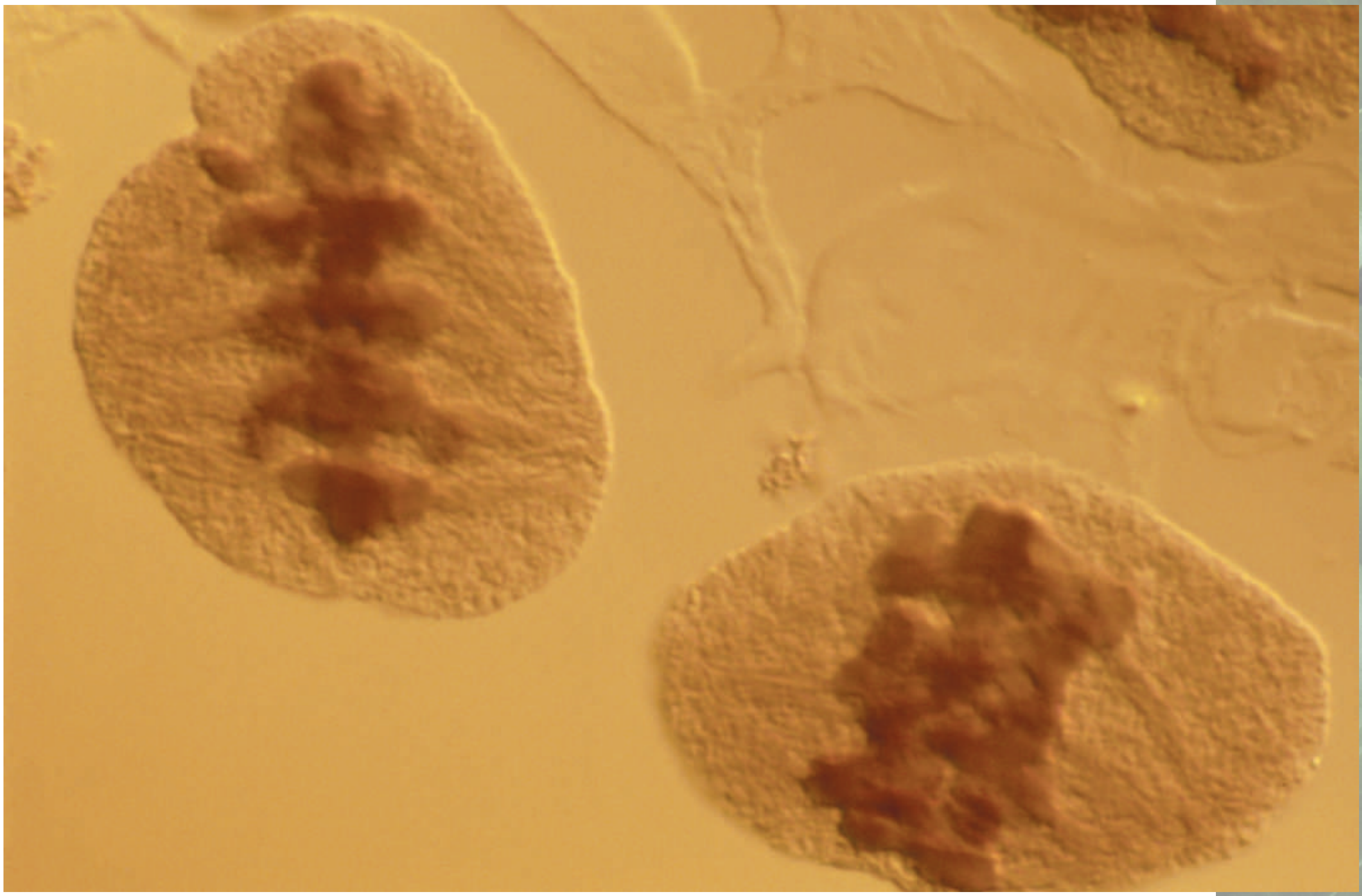
haploid having one set of chromosomes, versus having two (diploid)

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

diploid having two of each type of chromosome; twice the haploid number

During sexual reproduction two gametes, each of which is **haploid**, unite to form a single-celled **zygote**, which is **diploid**. As a consequence of the chromosome doubling that occurs during fertilization, at some point in the organism's reproductive cycle meiosis, or reductive cell division, must also occur to restore the haploid condition. In many organisms, including most animals, the zygote develops into a multicellular individual, and meiosis occurs during gamete production. In such organisms, gametes are the only haploid cells in the life cycle. In many algae and fungi, in contrast, the diploid zygote undergoes meiosis immediately to form haploid cells, called spores. Spores subsequently grow into multicellular haploid individuals. In both of these life cycles there is only one multicellular phase. In some algae and in all plants, however, there are actually two multicellular phases, one haploid and one diploid, which alternate with each other in the life cycle. This type of reproductive cycle is referred to as alternation of generations.

In organisms with alternation of generations, the diploid generation, or sporophyte, is formed by mitotic divisions of the diploid zygote, just as in animals. When mature, the sporophyte produces asexual reproductive organs called sporangia. Meiosis within the sporangia produces the one-celled, haploid spores that are released when the sporangia open. Each spore then gives rise to a multicellular haploid individual, or gametophyte. The gametophyte produces the sexual reproductive organs, or gametangia, in which



A micrograph of the first metaphase of meiosis in cells of a member of the lily family.

haploid gametes are formed by **mitosis**. Gametes then fuse to form the zygote, completing the cycle.

Occasionally, sporophyte and gametophyte generations look identical, as in many red and some green and brown algae, in which case alternation of generations is described as isomorphic. In other algae and all plants, the two generations are structurally different, and alternation of generations is said to be heteromorphic.

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

It is notable that isomorphic alternation of generations occurs only in certain algae and aquatic molds, while heteromorphic alternation of generations is the rule in land plants. In bryophytes the gametophyte is the ecologically persistent, independent generation, and the sporophyte is ephemeral and dependent upon the gametophyte for its nutrition. In all other plants the sporophyte dominates the life cycle. The fern gametophyte, for example, is a small thalloid plant, which is soon destroyed by the growth of the large, leafy sporophyte. In **gymnosperms** and **angiosperms**, the gametophyte is reduced to but a few cells of the pollen grain (the male gametophyte) and the embryo sac (the female gametophyte).

gymnosperm a major group of plants that includes the conifers

angiosperm a flowering plant

Two theories have been proposed to explain how alternation of generations evolved. Both theories hypothesize that the haploid generation is ancestral and that the diploid generation developed as a consequence of mitosis replacing immediate meiosis in the unicellular zygote. One theory proposes that originally the developmental potential of the diploid zygote was identical to that of the haploid spores, resulting in isomorphic sporophytes and gametophytes. Sporophytes became structurally different from gametophytes as a result of spores and zygotes being exposed to different environmental pressures. In land plants, for example, spores are released as unicells into the environment, while zygotes begin their development within the confines of the female gametangium. As a consequence, gametophytes, which develop from spores, and sporophytes, which develop from zygotes, are structurally very different.

The second theory proposes that the sporophyte generation evolved gradually by stepwise delays in zygotic meiosis, accompanied by the elaboration of vegetative diploid cells. The first sporophytes were little more than single sporangia, probably embedded in the much larger gametophytes. As evolution progressed, sporophytes became larger and larger, and gametophytes became more and more reduced. Even today, there is no consensus as to which theory best explains the diversity seen in modern organisms. SEE ALSO Algae; Angiosperms; Bryophytes; Ferns; Gametophyte; Gymnosperms; Reproduction, Fertilization and; Reproduction, Sexual; Sporophyte.

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Reproduction, Asexual

Although sexual reproduction is more frequent, asexual reproduction also commonly occurs in the plant kingdom. The technical term for asexual reproduction in plants is *apomixis*, derived from *apo* meaning "without," and *mixis* meaning "mingling." Apomixis thus refers to the fact that asexual reproduction lacks the mixing of genes that occurs in sexual reproduction. In apomixis, a new individual is produced by a single parent without pollination or mixing genetic material. A familiar example of apomixis is the production of new plants by the growth of horizontal stems (runners) in strawberries (genus *Fragaria*). Other familiar plants with asexual reproduction include blackberries (genus *Rubus*) and dandelions (genus *Taraxacum*), both of which produce asexually formed seeds. Apomixis is of great interest to plant breeders, because it allows the production of exact genetic duplicates of plants with favorable characteristics.

Asexual reproduction in plants is divided into two general types: vegetative reproduction and agamospermy. Vegetative reproduction refers to the formation of new plants by the growth of specialized structures that can survive after physical separation from the parent. Examples include growth by above- or below-ground stems (called stolons and rhizomes), and layering, in which the stem of a woody plant forms roots upon contact with the soil. Fragments of some plants can also grow to form new individuals. Poplar trees (genus *Populus*), for example, often shed branches that become rooted and produce new trees below the parent. Poplar trees can be easily **propagated** by simply cutting off branches and planting them directly in the ground.

propagate to create more of through sexual or asexual reproduction

The feathery parachutes of dandelion seeds (*Taraxacum officinale*) are the result of agamospermy.

Asexual reproduction by seed, called agamospermy, occurs when a single parent plant forms seeds without pollination. Agamospermy thus differs from self-pollination, in which pollen produced by a plant fertilizes its own ovules. Asexually produced seeds also differ in their development from typical, sexually produced seeds. In some plants, maternal **diploid** cells (which, in a normal seed, do not contribute to the new embryo) divide via **mitosis** and overgrow the developing ovule. The seed produced is thus genetically identical to the parent plant. A number of tropical fruit trees, such as mangos (*Mangifera* spp.), can reproduce in this manner.

diploid having two of each type of chromosome; twice the haploid number

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

colonize to inhabit a new area

Asexual reproduction is thought to be an important adaptation for plants that **colonize** open areas and harsh environments and, as such, is perhaps most common in plant species in arctic and alpine environments. The advantage may be that an asexually reproducing individual reaching a new area can always reproduce, even if no other plants of that species are present. Asexual reproduction also means that a plant's offspring will share 100 percent of its genes, while sexually produced offspring share only 50 percent of their genes with each parent. Evolutionary theorists have argued that, all other things being equal, this should act to favor asexual reproduction, since a parent thereby guarantees that all of its genes are represented in the next generation.

The main disadvantage of asexual reproduction is lack of genetic variation. For example, a disease or pest that has a large effect on one individual may be able to quickly infect all other individuals that share the same exact genetic makeup. In the long run, asexual reproduction may often be an evolutionary dead-end because plants that only reproduce asexually cannot recombine genes to produce new genetic variants. SEE ALSO PROPOGATION; REPRODUCTION, SEXUAL; STEMS; TISSUE CULTURE.

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Reproduction, Fertilization and

Gametes in plants—unlike those of animals—are not produced directly by meiotic division of a **diploid** organism, but by an entirely different haploid plant, in a process known as alternation of generations. In this process, embryos grow into **sporophytes**, and sporophytes release **haploid** spores. Spores grow into **gametophytes**, and gametophytes release gametes. Gametes fuse to form embryos.

diploid having two of each type of chromosome; twice the haploid number

sporophyte the diploid, spore-producing individual in the plant life cycle

haploid having one set of chromosomes, versus having two (diploid)

gametophyte the haploid organism in the life cycle

In mosses and liverworts, the embryo produces a small, but visible, sporophyte in which thousands of spores are produced through **meiosis**. The sporophyte that we see—the capsule and stalk of the moss—remains dependent on the dominant gametophyte (which is the vegetative moss plant).

meiosis division of chromosomes in which the resulting cells have half the original number of chromosomes

In ferns and so-called fern allies, the embryo produces a large sporophyte as the dominant generation (which is recognized as the vegetative plant). Keen observation is needed to see the free-living fern gametophytes, as they rarely reach 1/4 inch, but this is where sexual reproduction occurs in these plants.

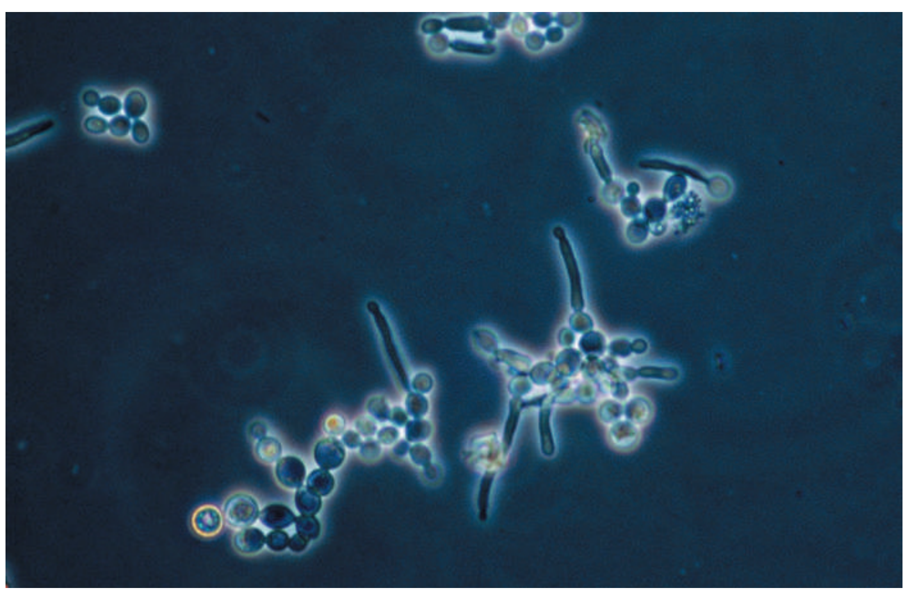
flagella threadlike extension of the cell membrane, used for movement

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

In mosses, liverworts, and ferns, the sperm cells have **flagella** and can swim. Sperm cells are released under moist conditions. Often the sperm are helped by being splashed out of the sperm-producing organ to within swimming distance of the eggs. Just one egg cell is found in each archegonium, which is the female protective organ on the gametophyte. A chemical signal or erotactin may be produced that attracts the sperm cells. When the egg cell is fertilized, it forms the **zygote**, which divides to form the embryo.

nonmotile not moving

In seed plants, the gamete-producing organs are highly protected and dependent on the sporophyte. Sperm cells form inside male gametophytes, known as pollen. The egg cells form inside female gametophytes, which in turn are located inside ovules. Each pollen grain forms only two sperm cells. The more primitive seed plants—*Ginkgo* and the cycads—have large sperm cells with hundreds or thousands of flagella. Most seed plants, however, have sperm that lack flagella and are **nonmotile**. Once pollination occurs, the



Magnification of pollen reveals the growth of sperm-conveying tubes from the microspores.

False color scanning electron micrograph of two young turnip (*Brassica campestris*) embryos seven days (small) and twelve days (large) after fertilization. Each has a well-developed root (brown) and a shoot embedded between two embryonic leaves, or cotyledons (green). The structure at the tip of the larger embryo's root is the remnant of the suspensor, which delivers food for the developing embryo from the mother plant.

pollen germinates and forms a tube. Nonmotile sperm cells depend on pollen tube growth for their transportation. Guided by chemical signals, the pollen tube grows over and through protective layers and deposits the sperm cells precisely next to the egg cell.

The egg cell is located within the ovule. In **gymnosperms** (e.g., conifers), the ovule contains a large female gametophyte with multiple archegonia and eggs. In **angiosperms** (flowering plants), the female gametophyte—reduced to one egg and six other cells—is known as an embryo sac. One of the two cells (called synergids) located next to the egg receives the successful pollen tube. Sperm cells are discharged from the pollen tube near the egg cell, and soon fuse with the egg cell to form the embryo. In angiosperms, a second sperm fuses with the central cell to form a nutritive **endosperm** during double fertilization. Fusion of sperm cells with each egg cell and central cell is required to produce the nutrition-rich endosperm needed for development of the embryo in flowering plants.

gymnosperm a major group of plants that includes the conifers

angiosperm a flowering plant

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

During fertilization in plants, male and female gametes: 1) contact one another; 2) adhere; 3) fuse their cells; and 4) fuse their nuclei. Fertilization triggers later embryo development. SEE ALSO BRYOPHYTES; FERNS; FLOWERS; FRUITS; POLLINATION BIOLOGY; REPRODUCTION, ALTERNATION OF GENERATIONS AND; REPRODUCTION, ASEXUAL; REPRODUCTION, SEXUAL; SEEDS.

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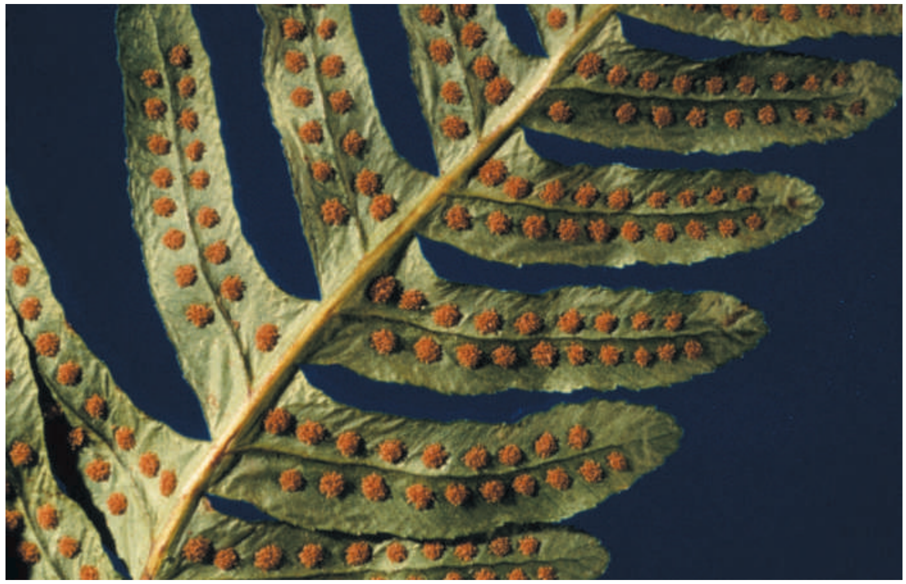
Reproduction, Sexual

Sexual reproduction is a fundamental process in plants that involves the production of egg and sperm followed by their fusion to form a **zygote**, which then divides and eventually develops into a new plant. Sexual reproduction

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual



Seed spores along the ribs of a fern leaf.

in flowering plants involves four sequential processes: sporogenesis, gametogenesis, pollination, and fertilization, all of which occur within the reproductive organs (the anthers and ovules) of the flower. Anthers are the site of (male) pollen formation, and ovules are the site of (female) egg formation.

Sporogenesis and Gametogenesis

Sporogenesis, or spore formation, begins with the differentiation of specialized spore mother cells within the anthers and ovules. The spore mother cells are unique because they undergo **meiosis**, a division that reduces the chromosome number by one-half, or from **diploid** to **haploid**. The haploid spores produced by meiosis in the anthers are called microspores (small spores), while those in the ovules are called megaspores (big spores).

meiosis division of chromosomes in which the resulting cells have half the original number of chromosomes

diploid having two of each type of chromosome; twice the haploid number

haploid having one set of chromosomes, versus having two (diploid)

gametophyte the haploid organism in the life cycle

During male gametogenesis, each microspore divides twice to produce a pollen grain, or mature male **gametophyte**, that consists of only three cells: two sperm cells and one vegetative cell. Female gametogenesis is slightly more complex. Of the four haploid megaspores formed following meiosis of the female spore mother cells, one typically divides four times to produce an eight-nucleate, seven-celled embryo sac, or mature female gametophyte. One of these cells becomes the egg.

Fertilization

pistil the female reproductive organ

Following gametogenesis, the sperm within the pollen grain must somehow reach the egg, which is buried within the ovary of the flower, before fertilization can occur. Flowering plants have evolved numerous adaptations that aid in the transfer of pollen to the tip of the **pistil**, or stigma. This process is referred to as pollination, and can be mediated by wind, insects, bats, or rodents. Once the pollen reaches the stigma, which is often sticky or hairy to trap the pollen grain, the pollen grain swells and germinates. It then sends a tip-growing tube through the style of the pistil to the egg. The vegetative cell of the pollen aids in tube growth. Once the tip of the pollen tube reaches the egg, it discharges the two sperm cells. One sperm cell fuses with the egg to form the diploid zygote, while the other sperm cell fuses with two nuclei that reside very close to the egg cell within the embryo sac. The triploid cell that results from this second fertilization event divides to form triploid **endosperm**, which is starchy material stored in the seed and provides nutrition for the developing embryo. Coconut milk and cornstarch are familiar examples of endosperm.

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

Although not all plants produce flowers or seeds, all land plants do form gametophytes of various shapes and sizes. In many lower plants, such as mosses and ferns, the haploid spores are shed from their parent and can remain **dormant** for many years. Once in a favorable environment, the spores germinate and divide to form a multicellular gametophyte that develops independently of the parent plant. Each gametophyte produces **motile** sperm and **nonmotile** egg cells. Until it develops a root system, the young embryo remains attached to and dependent upon the gametophyte. Because the gametophytes of these plants lack water-conducting tissues and require water for the sperm to swim to the egg, they can only be found in places that are damp for at least part of the year. While the fern gametophyte is small (0.25 inches), the moss gametophyte is the lush green carpet we think of as the moss plant.

dormant inactive, not growing

motile capable of movement

nonmotile not moving

Evolution of Sexual Reproduction

Most flowering plants produce "perfect" or hermaphroditic flowers with both male and female parts and can readily self-fertilize. One consequence of self-fertilization is inbreeding, which can have negative effects on offspring because they have a high probability of being homozygous for lethal recessive mutations. To avoid self-fertilization, flowering plants have evolved a number of adaptations or modifications to promote out-crossing, or mating between two individuals. Among these are genetic incompatibility, temporal (time-related) separation of pollen and egg maturation, as well as physical separation of the sexes into different flowers or individuals. Monoecious ("one house") plants, such as maize (corn), produce unisexual male flowers or female flowers, but both types are present on the same plant. Dioecious ("two house") plants, such as holly, produce unisexual male or female flowers on different plants. In some dioecious species, the sex of the individual is determined by sex chromosomes, while in other species, the sex of the flower is determined normally, and can be manipulated by applying plant growth hormones. Monoecious and dioecious species are thought to have evolved from species that produced perfect flowers.

Scientists have only recently begun to study and identify the genes that are involved in the evolution of reproductive structures in plants by studying the evolution of maize. The domestication of modern maize (*Zea mays* spp. *mays*) from its wild **progenitor** species, teosinte (*Zea mays* ssp. *parviglumis*) began approximately ten thousand years ago. During this period, agriculturists selected for traits, such as the monoecious condition, that affect the reproductive structures of this plant. What is known at this point is that the large differences one observes between maize and teosinte are attributed to differences in a very small number of genetic **loci**. Once all of these loci have been cloned, scientists will be able to understand at the molecular level how reproductive characteristics evolve.

progenitor parent or ancestor

loci (singular: locus) sites or locations

Advantages and Disadvantages of Sexual Reproduction

propagate to create more of through sexual or asexual reproduction

morphologically related to shape or form

Many plants **propagate** themselves readily by asexual reproduction. Cattails (*Typha latifolia*), for example, vegetatively multiply by underground stems to form large stands of genetically identical individuals. Why do such plants expend great amounts of energy to produce the floral structures necessary for sexual reproduction when they can successfully reproduce without sexual reproduction? Scientists believe that sexual reproduction is widespread among living organisms because the advantages it provides to the species outweigh the disadvantages. The key to understanding these advantages has to do with the genetic processes that occur during meiosis and fertilization. During meiosis, homologous pairs of chromosomes (each chromosome of a pair previously contributed by each parent) pair with each other and recombine, or exchange genetic material. The resulting haploid cell or gamete contains only one of each chromosome pair, yet each chromosome has a mixture of genetic material from both parents. This mixing of genetic information during sexual reproduction results in offspring that are genetically and **morphologically** different (compare the appearance of genetically identical twins to nonidentical siblings). These differences allow natural selection and adaption to changing conditions. Sexual reproduction thus serves two purposes: in many cases, it is necessary to propagate the species and in all cases is needed to maintain genetic diversity within a species. The long-term consequence of a species that lacks genetic diversity between its members is extinction. SEE ALSO BREEDING SYSTEMS; CORN; FLOWERS; POLLINATION; REPRODUCTION, ALTERNATION OF GENERATIONS AND; REPRODUCTION, FERTILIZATION AND; REPRODUCTION, SEXUAL; SEEDS.

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Rhythms in Plant Life

The natural environment is always changing, sometimes predictably, but more often not. Unlike animals, plants cannot move away or seek shelter from unfavorable conditions, so it is crucial that they are able to adapt quickly to such changes. Unpredictable changes include daily temperature, rainfall, and amount of light, and plants have developed a range of responses to deal with these changes. However, some aspects of the environment change regularly, such as the seasons; the monthly waxing and waning of the moon; the cycle of the tides coming in and out; and, of course, the daily changing of light and dark. It is therefore not surprising that, like most other living organisms, plants have evolved so that their behavior or development changes in synchrony with these predictable changes in the environment.

Types of Rhythms

A rhythm is a process that changes regularly and continuously. It can best be represented as a wave, as with light or radio waves, or on a graph where response is plotted against time. The distance between successive peaks or troughs of the wave is then referred to as the period of the rhythm. Rhythms in plants have a range of periods. For example, the circular growth of some stems has a period of less than one hour, but the flowering in some bamboos has a period of seven years. The most widespread rhythms are those with a period of about twenty-four hours, referred to as circadian rhythms (from the Latin *circa*, meaning "about," and *diem*, meaning "day"). Some examples of processes that show circadian rhythms are photosynthesis, stomatal movements, root pressure, nitrogen fixation, bioluminescence, cell division, leaf movements, flower opening, and fragrance emissions. Circadian rhythms, which match the daily twenty-four-hour cycle of day and night, have almost certainly been selected for during evolution, and it is thought that they are the visible expression of a biological clock in plants.

A boojum tree in Mexico during the dry season. The plant adapts to seasonal changes in precipitation by restricting the growth of its foliage in the dry season.

Characteristics of Circadian Rhythms

Perhaps the first observation of a circadian rhythm associated with a plant was made by Androsthenes, scribe to Alexander the Great, who noticed that the leaves of certain trees were elevated by day and drooped at night. More recently, an eighteenth century French astronomer, Jean de Mairan, observed that the leaves of certain "sensitive" plants, probably mimosa, continued to open and close even during long periods of darkness. In the first half of the twentieth century the German plant physiologist Erwin Bünning made detailed observations of the movement of bean leaves. He confirmed that the leaves continued to move up and down in constant darkness, and established that the period was 25.4 hours.

Bünning's work also established the most important property of these rhythms, which is that they are truly internal and thus generated by the plant. The rhythm continues running under constant environmental conditions (called a free running rhythm), which indicates that it is driven from within and not by a rhythm of the environment. Another important property is that the phase of the rhythm can be changed by light. This means that every day, at the onset of daylight (dawn) the rhythm is reset so as to coincide with the daily light-dark cycle in the environment. This phenomenon is known as entrainment and is crucial to the functioning of the biological clock.

Nature of Biological Clocks

The biological clock allows an organism to match its internal system with the time of day, so that in some sense it could be said to "know" what the time is. Inside every cell are processes that change rhythmically and that drive the observed rhythms. The actual mechanism of the clockwork is not known, although recent research in organisms such as fruit flies and fungi suggests that a cycle of gene transcription and protein synthesis is an important part. Another part of the clock is one or more photoreceptors through which light entrains or sets the clock to match up with the daily light cycle. Having many internal processes matched with the daily light

A boojum tree in Mexico during the moist season. The plant adapts to seasonal changes in precipitation by maintaining foliage in the moist season.

cycle allows the plant to anticipate changes that occur during the day, such as switching on genes associated with photosynthesis before the onset of daylight. It also allows them to carry out incompatible processes at different times, such as nitrogen fixation and photosynthesis in unicellular **cyanobacteria**.

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

Having a biological clock that is reset by light and dark means that plants can measure the length of day and/or night. This also allows them to tell what season it is by whether days are getting longer or shorter. Many developmental responses are triggered by changes in the length of day, a type of behavior termed photoperiodism. While some changes occur in response to shortening of the daylength, others occur as days get longer. These two types of photoperiodic response were first recorded for the induction of flowering and led to the classification of plants as short-day plants or long-day plants. Those plants that do not respond to daylength are called day-neutral plants.

There are several advantages to having developmental responses controlled by daylength. For flowering, it means that members of a **population** will flower at the same time, which increases the chances of outbreeding and thus genetic recombination. If a pollinating insect's behavior is also photoperiodically controlled, this further improves the chance of successful pollination. Another example of the survival value of seasonal timing of flowering is that woodland plants can flower and set seed before the dense leaf canopy is formed. Other changes that occur in response to daylength include the formation of storage organs such as bulbs or tubers, the onset of dormancy, and the development of cold hardiness in trees. These changes help plants survive through the winter and are triggered by the shortening daylength during autumn. SEE ALSO Photoperiodism; Senescence; Tropisms and Nastic Movements.

population a group of organisms of a single species that exist in the same region and interbreed

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Rice

Rice (*Oryza sativa*) is a staple food for nearly half of the world's population. Rice is a member of the grass family, which also includes wheat, corn, sorghum, barley, oats, and rye. Unlike other grains, rice is well adapted to aquatic environments. Rice originated in Southeast Asia, where archeological evidence—including carbon-dated grain imprints in pottery shards—indicates that it was under **cultivation** at least six thousand years ago. Cultivated rice consists of two subspecies, *O. sativa* subsp. *indica*, which is grown in the tropics and subtropics, and *O. sativa* subsp. *japonica*, which is grown in temperate regions.

cultivation growth of crop plants, or turning the soil for this purpose

Although rice is grown in 115 countries, over 90 percent of the crop is in Asia. In 1999 world rice area was 153 million hectares (Mha), and total

Terraced rice paddies in Ubud, Bali.

production was 589 million metric tons (Mmt). India had the largest area, 43.0 million hectares, and China was second with 31.7 million hectares. However, yields in China averaged 6.33 metric tons per hectare (mt/ha) compared to 2.97 metric tons per hectare in India, so China had the largest total production. Other leading rice countries in 1999 were: Indonesia, 11.5 million hectares; Bangladesh, 10.5 million hectares; Thailand, 10.3 million hectares; Myanmar, 5.6 million hectares; Brazil, 3.7 million hectares; the Philippines, 3.9 million hectares; and Pakistan, 2.4 million hectares. The United States was far down the list at 1.4 million hectares, but with yields of 6.65 metric tons per hectare was well ahead of the world average yield of 3.84 metric tons per hectare.

Except for a small amount for seed, all rice is used for human consumption. Most rice is consumed in the country where it is grown, with about 5 percent going into international trade. In the late 1990s, five countries dominated export markets, in the following descending order: Thailand, Vietnam, the United States, India, and Pakistan. About 40 percent of the U.S. crop is exported, with leading destinations being Latin America, Europe, Africa, and the Middle East.

Cultivation Techniques

Rice is grown under conditions ranging from full flood to rainfed upland conditions. Highest yields are obtained under flood, so the half of the world's rice area that is flooded produces 75 percent of the total crop. U.S. production is all flooded. Although rice is primarily a tropical or subtropical crop, it is grown from 53°N to 40°S. Interestingly, highest yields are obtained in high-latitude temperate areas such as Australia, Egypt, Korea, Italy, Spain, Uruguay, and the United States. High yields in the temperate areas occur because of longer day length, fewer storms, and relative freedom from the traditional diseases and insect pests of the tropics.

In the tropics and subtropics, rice is transplanted into flooded fields, following two or three weeks of initial growth in seedbeds. Most transplanting is by hand, but machine transplanting is becoming popular as labor costs increase. In temperate regions rice is direct seeded, either with grain drills into soil or water seeded by airplane into flooded fields. In all cultivation systems, highest yields are obtained by keeping the floodwater on for as much of the season as possible. Fertilizers are applied before and during the growing season, and weeds are controlled by handweeding and herbicides. About two or three weeks before harvest, fields are drained. In the tropics and subtropics, harvest is by hand while in temperate regions grain combines are used. All harvesting techniques involve threshing the grains from the **panicles** at the top of the plant. Man-hours per hectare for producing rice are as high as 300 in hand-transplanting cultivation, but are as little as 20 in mechanized cultivation in the United States. Total length of the growing season is 100 to 130 days. In the tropics two or even three rice crops may be produced per year, but in temperate areas only one crop is grown per year.

panicle the grain-bearing head of the plant

Harvest and Milling

At harvest, rice grain is called paddy or rough rice. In preparation for consumption, the hulls are removed by dehulling machines. Hulls, which are 18 percent by weight of paddy, have high silica content and are of little value except for onsite fuel or mixing into compost materials. Hull removal produces brown rice, which then is milled to remove the grain's outer layers, called bran, 10 percent by weight of paddy, and white rice, 72 percent by weight of paddy. Edible oil, about 2 percent by weight of paddy, is extracted from the bran and the remainder of the bran goes into pet food. Virtually all human consumption is as milled white rice, except for a small amount as brown rice in health food markets. In much of the world the milled rice goes into food use. In the United States, 81 percent of the domestic use of rice is for food, 15 percent for brewing, and the remaining 4 percent for seeding the next crop.

Worldwide, per-capita consumption of milled rice is 84 kilograms per year. Per-capita consumption is declining in developing nations as they become more affluent. In the United States, per-capita consumption is now 12 kilograms, which represents a doubling since the early 1980s. The increase in the United States is due to growth in ethnic groups who prefer rice, to recognition that rice is a healthful food, and to rice industry promotion efforts.

Rice and the Green Revolution

The Green Revolution began in the 1960s, when tall, **lodging**-susceptible rice and wheat varieties were converted to semidwarf varieties. The semidwarfs stand up better, produce more panicles per unit area, are more responsive to fertilization, and yield more. For example, in the pre-Green Revolution era of the early 1960s, world average rice yields were about 2 metric tons per hectare, compared to the 1999 average of 3.8 metric tons per hectare. The combination of high yielding semidwarfs plus more intensive cultural practices has driven the increase.

lodging falling over while still growing

Wild Rice

In North America the term *wild rice* refers to an unrelated aquatic crop, *Zizania palustris*, which is grown in cooler areas such as Manitoba, Canada, and Minnesota. Small portions of *Z. palustris* grain are blended into gourmet preparations of regular rice. In Asia the term wild rice refers to the twenty related species of *Oryza*, which also are called weedy rice. One of these related species, *Oryza glaberrima*, is cultivated in Africa, but is being rapidly replaced by the higher-yielding *O. sativa*. The wild or weedy species of *Oryza* serve as sources of resistance to diseases and insects of cultivated rice. SEE ALSO AGRICULTURE, HISTORY OF; AGRICULTURE, MODERN; BORLAUG, NORMAN; ECONOMIC IMPORTANCE OF PLANTS; GRAINS; GRASSES; GREEN REVOLUTION.

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Roots

Plants have three organs: roots, stems, and leaves. Growth, flowering, food production, and storage all depend on the activities of these three organs. The combination of stems and leaves makes up the shoot system that is usually visible because it grows above the ground and gives rise to flowers, fruits, and seeds. Roots, on the other hand, are often underground, but the root system can be every bit as massive as the aboveground shoot system. An active root system makes it possible for the plant to carry out growth, photosynthesis and other chemical reactions, branching, flowering, fruiting, and seed production.

Roots are so critical to plant survival that a sprouting seedling devotes its first days to root growth before allowing leaves to pop out of the seed. During this time of early germination, the root anchors the plant in the soil and begins to deliver a reliable water supply to the growing seedling. In dry climates, the time taken by roots to find reliable water can take years. The two-year-old sprouts of some California oaks can have a three-foot long root, while their shoots are restricted to only two leaves. In the Namib Desert of Southwest Africa, *Welwitschia* plants spend their entire one-hundred-year life growing underground roots, leaving only two leaves on the plant even after a century of growth. These examples illustrate the priority placed on root growth over shoot growth in specialized (dry) environments. In moister climates, roots will still be the first organs to emerge from seeds, but leaves will follow them within about ten days.

The primary root, or radicle, is the first root to emerge from the seed. From there, the plant can develop a taproot system or a fibrous root system. In dicotyledons, including most trees (except palms), the radicle grows into a strong taproot that sends small branch roots out to the side. In monocotyledons, especially grasses and palms, the radicle stops growing early on and many roots emerge from the seed, each forming similar-sized branch roots that combine into a fibrous root system. Long taproots allow plants to reach deep reliable water supplies, while fibrous roots absorb surface water before it evaporates. Fibrous roots also stabilize soil, reducing erosion.

Root Functions

Most root functions take place in the youngest part of roots, usually 10 centimeters from the growing root tip. Four activities are accomplished in that area:

Roots Stabilize the Plant. Roots anchor plants in soil by pressing between soil particles. Loose or wet sand or mud makes it much harder for roots to

Roots of an elephant ficus tree spread out on the surface from the base of its trunk.

secure mechanical anchorage. Trees topple when high winds sweep sandy areas, wetlands, or rainsoaked slopes. In free-floating aquatic plants, such as duckweed and water hyacinth, roots stabilize the plant by dangling into the water, acting as a keel to keep the leaves upright and preventing plants from toppling over. When roots are experimentally removed from water hyacinth, the plants tip over and die.

Roots Absorb Water and Minerals. Roots absorb water and minerals and transport them to the shoot. In a root system, each root elongates from its tip, entering new soil that can be exploited as an undepleted source of minerals and water. Delicate single-celled root hairs grow from the epidermis and greatly increase the root surface area devoted to absorption. Conditions that harm root hairs in the soil will **impede** nutrient uptake and harm the entire plant as leaves turn yellow and plant growth slows. Soil **compaction** and salt accumulation are two environmental factors that harm plants by killing root hairs. In 1999, decline in fruit quality from date orchards in Southern California was slowed by reducing tractor traffic near the trees. This decreased the likelihood of crushing root hairs on the shallow fibrous root systems of date palms.

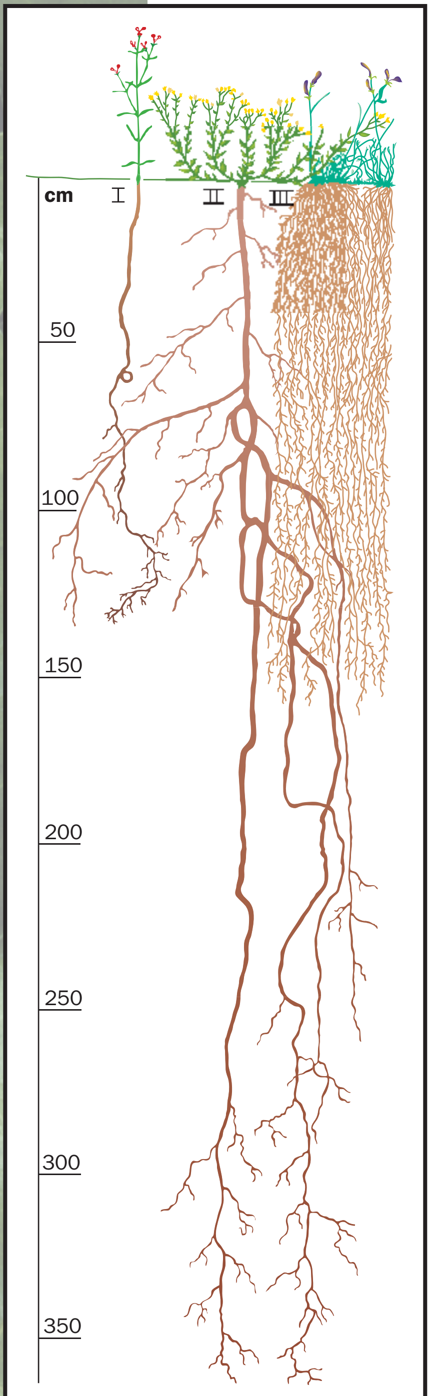
impede slow down or inhibit

compaction compacting of soil, leading to loss of air spaces

There are more than fifteen elements needed by plants to grow. Of these, roots absorb nitrogen (N), phosphorus (P), and potassium (K) in the largest amounts. The soil minerals most commonly available for root uptake are those that are stuck onto tiny colloid particles in the soil. Colloids are abundant in clay and in broken-down compost. They enhance soil fertility by anchoring minerals in the soil and preventing them from being washed (leached) down and away from plant roots. Colloids are negatively charged particles, allowing minerals with positive charges (potassium, calcium, iron, etc.) to stick to them. Roots can free these stuck minerals by releasing protons (H^+) from inside the root and exchanging them for positively charged minerals on the colloid surface in a process called cation exchange. The cation exchange capacity of a soil is a strong indicator of soil fertility, the ability of a soil to provide roots with essential minerals over long periods of time. Acid rain (high in H^+) in Europe and Northeastern North America (Canada and the United States) decreases soil fertility by displacing minerals from soil colloids, thereby lowering the soil's exchange capacity.

Roots Attract Microbes. The roots of many species attract beneficial soil microbes by secreting a paste (mucigel) rich in sugar. The sugars support large populations of soil bacteria and fungi that help roots absorb minerals, especially nitrogen and phosphorus. The bacteria involved are nitrogen fixing bacteria. The fungi are mycorrhizae, long threadlike fungi that attach to plant roots and form a bridge connecting roots to minerals that would have been out of reach of the shorter root hairs. Almost all major agricultural crops have fungi or bacteria associated with their roots. Plants invest up to 10 percent of all food made by leaves to the paste they secrete out of roots. In some cases, the mucigel can feed more than just microbes. In lava tubes such as the Kaumana caves of Hawaii, entire populations of insects live in total darkness, fed only by mucigel from roots pushing through the cave ceiling.

Roots Store Food. Since roots are underground and away from light, making their own food by photosynthesis is impossible. Instead, sugar made by



Comparisons of roots: tap (I and II) and fibrous (III). Redrawn from Kutschera, 1960.

commodities goods that are traded, especially agricultural goods

leaves is transported to roots for storage as starch. The stored food can power root growth, or it can enlarge roots in some cases, turning them into economically important **commodities** such as cassava (*Manihot*) from West Africa and the Caribbean, sweet potato (*Ipomoea*), and ginseng (*Panax*) from China and North Carolina.

Root Anatomy

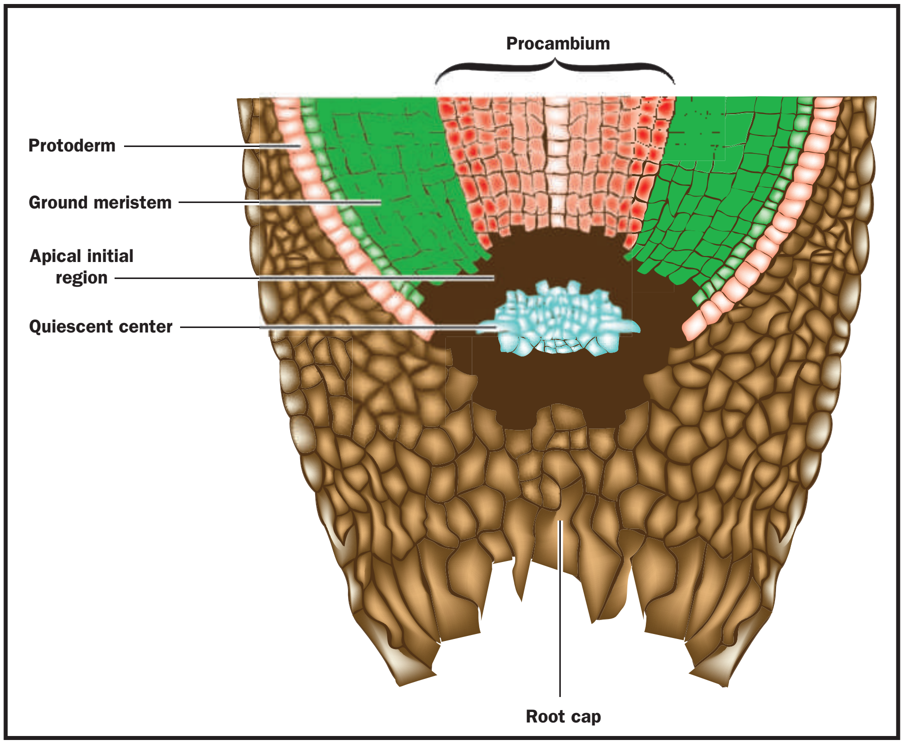
Four features help distinguish roots from shoots. In roots: 1) a protective cap covers the growing tip, 2) single-celled root hairs are present, 3) branching starts deep within the root, and 4) xylem and phloem alternate around the vascular cylinder.

The root cap protects the tender growing tip against **abrasion** by soil particles. By secreting mucilage, the cap may help lubricate passage of the growing root through the soil. The cap helps attract nitrogen fixing bacteria and mycorrhizal fungi by secreting sugars that feed them. Finally, the root cap detects gravity and directs most roots to grow downward in a process called gravitropism. Corn roots with caps removed by microsurgery grow in random directions until the cap regenerates, after which time they return to growing downward.

When viewed from the outside in, root cross sections show six tissues. The epidermis is the interface between the soil environment and the living root. There is no water-repellent **cuticle** over the epidermis of roots growing in moist media such as soil or water. Everything absorbed by the root must pass through the epidermis including water, minerals, and pollutants such as heavy metals and pesticides. The surface area devoted to uptake of water and minerals is greatly increased by single-celled root hairs extending from thousands of epidermal cells. Root hairs are especially important for water uptake from soil. Aquatic plants with ample supplies of water, such as *Elodea* and water chestnut (*Trapa*), produce no root hairs.

The root cortex contains food-storage cells usually filled with starch. The cortex is especially large in storage roots such as those of cassava, sweet potato, and tropical yam (*Dioscorea*). The cortex spans from the epidermis to the endodermis, which is the innermost layer of cortex. The endodermis helps regulate which **compounds** spread throughout the plant. Cell walls of mature endodermal cells contain a ribbon of wax called the Casparian band, which prevents water from passing from the cortex into the root vein through the cell walls. Instead, water (and the compounds dissolved in it) must pass through the cytoplasm of endodermal cells before it can spread throughout the plant. This allows the plasma membrane of endodermal cells to regulate which compounds pass deeper into the root. Calcium absorption is regulated this way, as is the uptake of pollutants, including soil-borne lead, which are known to accumulate at the endodermis and to pass no farther.

The root vein, or vascular cylinder, is at the center of the root. In dicotyledons, xylem with two to six armlike lobes in a starlike configuration is at the core of the root. In monocotyledons, there can be twenty or more xylem arms in a circle around a central pith. Patches of phloem are tucked between each of the xylem arms. Water and minerals absorbed by the root move upward through the root xylem to the above-ground shoot system. At



Parts of root cap and quiescent center. Redrawn from Moore et al., 1998, Figure 15.6.

the same time, in the phloem, the solution of sugars and other carbon compounds made by leaves moves down into the roots.

The pericycle occupies the space between the outmost reaches of xylem arms and the endodermis. It ranges from one to six cell layers wide. Branch roots develop from the pericycle. By combining mechanical force with parent cell breakdown, the young branch root pushes through the endodermis, cortex, and epidermis of the parent root before reaching the soil. Developing from the pericycle allows branch roots to connect to xylem of the parent root at the earliest stages of their development. Root branching increases in response to pockets of enhanced resources in soil, leading to root proliferation around fertilizer pellets, dissolving rock, decaying animals, buried reptile eggs, or water drops.

abrasion wearing away through contact

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

compound a substance formed from two or more elements

Root Growth

Roots grow 1 to 6 centimeters each day by cell division and cell elongation near their tip. Growth depends on oxygen and temperature. Air space takes up 30 to 50 percent of productive soil volume, and depletion of that space by soil compaction or by flooding will reduce or stop root growth. The growing root tip is organized into three distinct zones, with an inactive zone sandwiched between two actively dividing meristems. The cap meristem is a layer of rapidly dividing cells between the root cap and the root body. It maintains the root cap, whose tip cells are **abraded** by soil particles. Behind the cap meristem is a lens- or bowl-shaped group of cells that seldom, if ever, divide. This is called the quiescent center, and its roles are to produce growth regulators (including cytokinin) that regulate root growth, to provide a reserve of cells that can replace injured cells of the cap and body meristems, and to physically regulate the size of those meristems.

abrade wear away through contact

Behind the quiescent center is the body meristem responsible for creating all root tissues except the cap.

Modified Roots and Their Economic Importance

In warm climates where freezing is not a problem, roots can grow above ground where they assume diverse functions. Above-ground roots are well developed in orchids, fig trees, and mangroves growing throughout the tropics and subtropics.

epiphytes plants that grow on other plants

The orchid family includes climbing orchids and **epiphytes** that live on tree branches, close to sunlight but away from soil. Roots of the vanilla orchid emerge from the stem and support this climbing vine by twining around sticks and branches of trees. Roots of epiphytic orchids are out in the open where they have access to sunlight and rainwater, but not to soil. Long-term studies at Hummingbird Cay Tropical Field Station in the Bahamas show these orchids grow very slowly but live for decades. Their aerial roots have a spongy multilayered epidermis called velamen that enables roots to store water from rain and bark runoff. To the inside of the velamen the cortex is modified for photosynthesis, performing a function usually restricted to leaves. Photosynthesis by the elaborate green roots of epiphytic orchids in the tropics and Japan compensates for the reduced leaves in these plants.

Ficus trees such as figs and banyans use buttress roots and stilt roots to support large canopies atop shallow tropical soil. Buttress roots resemble rocket fins at the bottom of large tree trunks. They develop from the fusion of the upper side of a horizontal root with the vertical tree trunk in response to tension as the tree leans away from the developing buttress. Trees growing on hillsides show larger buttresses on the uphill side of the trunk than on the downhill side. Buttresses are prominent on Brazilian rubber tree (*Hevea*), and kapok (*Ceiba*). Stilt roots develop from horizontal branches and grow down to the soil where they thicken and become long-lived supports for the tree canopy.

ecosystem an ecological community together with its environment

Mangroves are trees living in tropical coastal areas. Their roots are of enormous value in stabilizing tropical coast lines against typhoons, hurricanes, and wave action, and they give refuge to young stages of commercially important fish. The global value of such **ecosystem** services provided by mangroves was estimated in 1997 to exceed $600 billion. To help restore damaged environments, mangroves are being replanted in Vietnam, the Philippines, and Mexico. Mangrove roots allow these coastal trees to grow in shifting sand and oxygen-poor soil. The stilt roots of red mangrove (*Rhizophora*) spread down into sand from dozens of canopy branches, thereby stabilizing the tree. Pores, called lenticels, on the root surface allow oxygen to enter the aerial part of the root and diffuse down to submerged tissues in oxygen-depleted soil. Massive intertwined root systems of red mangrove forests prevent hurricanes from removing acres of land from south Florida and the Caribbean. The root system of black mangrove (*Avicennia*) has at least three root types. Underground cable roots radiate horizontally from the central tree trunk and stabilize the tree. They produce upward-growing roots (pneumatophores) that grow out of the soil and act as snorkels to bring oxygen into belowground roots. Feeder roots branch from the base of each pneumatophore where their large surface area absorbs minerals from the soil. SEE ALSO Anatomy of Plants; Compost; Epiphytes; Nitrogen Fix-

ation; Nutrients; Orchidaceae; Tissues; Tropism; Vascular Tissues; Water Movement.

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Rosaceae

The family Rosaceae consists of about one hundred **genera** and three thousand species. It is distributed throughout the world, being especially common in North America, Europe, and Asia. Many members of the family are woody shrubs or trees. Others are perennial herbs: the stems die back at the end of each season and the root lives on to produce new stems in following seasons. The flowers of Rosaceae are distinctive because of the presence of a hypanthium, a cup-shaped structure forming the base of the flower. The **sepals**, petals, and stamens are attached to the edge of the hypanthium, while the **pistil** or pistils (which develop into the fruit or fruits) sit in the bottom of it.

genera plural of genus; a taxonomic level above species

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

pistil the female reproductive organ

achene a small, dry, thinwalled type of fruit

One of the most conspicuous characteristics of Rosaceae is the variety of fruits produced by its species. Many Rosaceae have **achenes** and follicles, both of which are nonfleshy. Achenes contain one seed and have a hard fruit wall that does not split open at maturity, whereas follicles contain more than one seed and split open at maturity. Most fleshy fruits of Rosaceae are either drupes or pomes. A drupe (or stone fruit) contains one seed; the inner part of the fruit wall (the pit) is hard, and the outer fruit wall is usually fleshy. Peaches, plums, and cherries are examples of fleshy drupes, while almonds are nonfleshy. The fruits of raspberries and blackberries are clusters of many very small drupes. Pomes such as apples and pears are unusual fruits because the fleshy part does not develop from the pistil but from the hypanthium. The mature pistil containing the seeds is enclosed by the fleshy hypanthium. The fleshy part of the strawberry fruit is also not made from the pistil but from the base of the flower, which has expanded and become fleshy (accessory tissue). The fruits are achenes that are attached to the outside of the fleshy structure.

Rosaceae is very important economically. Many members of the family are important as ornamentals because of their foliage or flowers. Others are important components of diets in countries throughout the world because of

ECONOMICALLY IMPORTANT ROSACEAE SPECIES

Scientific Name	Common Name	Uses
Ornamental shrubs and trees		
Chaenomeles species	Flowering quince	Flower ornamental
Cotoneaster species	Cotoneaster	Foliage and flower ornamental
Crataegus species	Hawthorn	Foliage and fruit ornamental, hedgerows
Eriobotrya japonica	Loquat	Foliage ornamental
Kerria japonica	Kerria	Flower ornamental
Malus species	Crabapple	Flower ornamental
Prunus species	Flowering cherry	Flower ornamental
Pyracantha species	Firethorn	Foliage ornamental
Rosa species	Rose	Flower ornamental
Spiraea species	Bridal wreath	Foliage and flower ornamental
Ornamental herbs		
Alchemilla species	Lady's mantle	Foliage ornamental
Filipendula species	Meadowsweet	Foliage and flower ornamental
Geum species	Avens	Foliage and flower ornamental
Potentilla species	Cinquefoil	Foliage and flower ornamental
Food and wood plants		
Cydonia oblonga	Quince	Fruit
Fragaria species	Strawberry	Fruit
Malus domesticus	Apple	Fruit, wood
Mespilus germanica	Medlar	Fruit
Prunus species	Cherry	Fruit
Prunus species	Plum	Fruit
Prunus amygdalus	Almond	Fruit
Prunus armeniaca	Apricot	Fruit
Prunus persica	Peach	Fruit
Prunus serotina	Wild black cherry	Wood
Pyrus communis	Pear	Fruit, wood
Rubus species	Blackberry, raspberry	Fruit

the fiber, phytochemicals, and vitamins they contain. Much of the fresh fruit eaten by people in temperate regions (apples, pears, strawberries, and cherries, for example) are members of family Rosaceae. Some members of Rosaceae are large enough to be sources of wood. The wood of wild black cherry (*Prunus serotina;* the largest species of Rosaceae) is a desirable furniture wood, and the wood of pear is used to make musical instruments such as recorders. SEE ALSO Economic Importance of Plants; Fruits; Horticulture.

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S

Sachs, Julius von

German botanist
1832–1897

Julius von Sachs was born October 2, 1832, in what is now Poland. Although his family was very poor, his brilliance and constant hard work helped him become in his day the foremost authority on the new science of plant

physiology. He was made a member of many scientific societies and academies, and was awarded a grant of nobility that allowed him to use "von" before his name. Sachs published several books that became the definitive plant physiology references for many years. His *Lehrbuch der Botanik* (*Textbook of Botany*) went through many editions and is still read today.

physiology the biochemical processes carried out by an organism

Sachs's main scientific contributions to plant science came with his early research in the mid-1800s. He enjoyed lab research more than attending lectures in school and he worked with incredible energy and determination. Throughout his career, Sachs strove to find general principles and large concepts involved in botany, rather than focus on smaller, more specific questions. He used microscopic and chemical techniques to study three main areas of plant physiology: carbon use in plants, the mineral requirements of plants, and the effect of temperature on plants. This work laid the foundation for the study of plant physiology among his successors.

In examining the fate of carbon in plants, Sachs used an iodine test to show that carbon was first accumulated as starch in the leaves of plants. He also demonstrated that this accumulation occurred in the **chloroplasts** and that chlorophyll, light, and carbon dioxide were necessary for carbon fixation. Sachs also observed the way in which the carbon in starch was converted into different compounds in the plant, such as oils, sugars, and proteins. He was one of the first researchers to believe that **enzymes** did essential work in these metabolic conversions.

chloroplast the photosynthetic organelle of plants and algae

enzyme a protein that controls a reaction in a cell

Sachs developed a method to culture plants in water instead of soil, which allowed him to experiment with the nutrient content of the water he gave the plants. He used this technique to demonstrate that plants can grow with just water, the right nutrients, and sunlight. Many other scientists believed at first that he must have faked his results—they were certain that soil was necessary for plant growth. Later, of course, Sachs's pioneering research led to the development of **hydroponics** and the agricultural fertilizer industry.

hydroponic growing without soil, in a watery medium

Sachs's examination of the effects of temperature on plants showed that plants have minimum, maximum, and optimum temperatures at which they grow. These ideas became important later in the study of ecology.

As one of the founders of the modern study of plant physiology, Sachs developed new techniques and scientific instruments, and he helped make plant physiology into a scientific discipline with its own methods and laws. His great authority occasionally led him to be unfair in disagreeing with other scientists (including Charles Darwin) and just his disapproval of an idea could delay research into it. Despite this, Sachs made very important advances in the plant sciences and he was very well respected when he died in Germany on May 29, 1897. SEE ALSO DARWIN, CHARLES; HYDROPONICS; PHOTOSYNTHESIS, CARBON FIXATION AND; PHYSIOLOGIST; PHYSIOLOGY; PHYSIOLOGY, HISTORY OF.

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Savanna

ecosystem an ecological community together with its environment

Grass-dominated **ecosystems** that contain a significant number of widely spaced trees are termed savannas. Trees may make up as little as 5 percent or as much as 30 percent of the cover of all plants in savannas, but grasses and grasslike plants form a continuous ground cover. Originally, savanna was a term used to describe primarily tropical and subtropical grasslands, which usually have more woody plants than temperate grasslands. These tropical and subtropical savannas occupy large land areas. Almost 65 percent of Africa is covered by savanna, much of the northern region of Australia has savanna vegetation and South America has extensive savannas. Worldwide, estimated land cover by savanna is nearly 20 percent.

Savannas may be a product of climatic factors, they may result from unique soil types, or they may be narrow to broad transitional zones between forests and grasslands. Fire and periods of water limitation are present in all savannas whether they occur in the tropics or in temperate zones.

Tropical and Subtropical Savannas

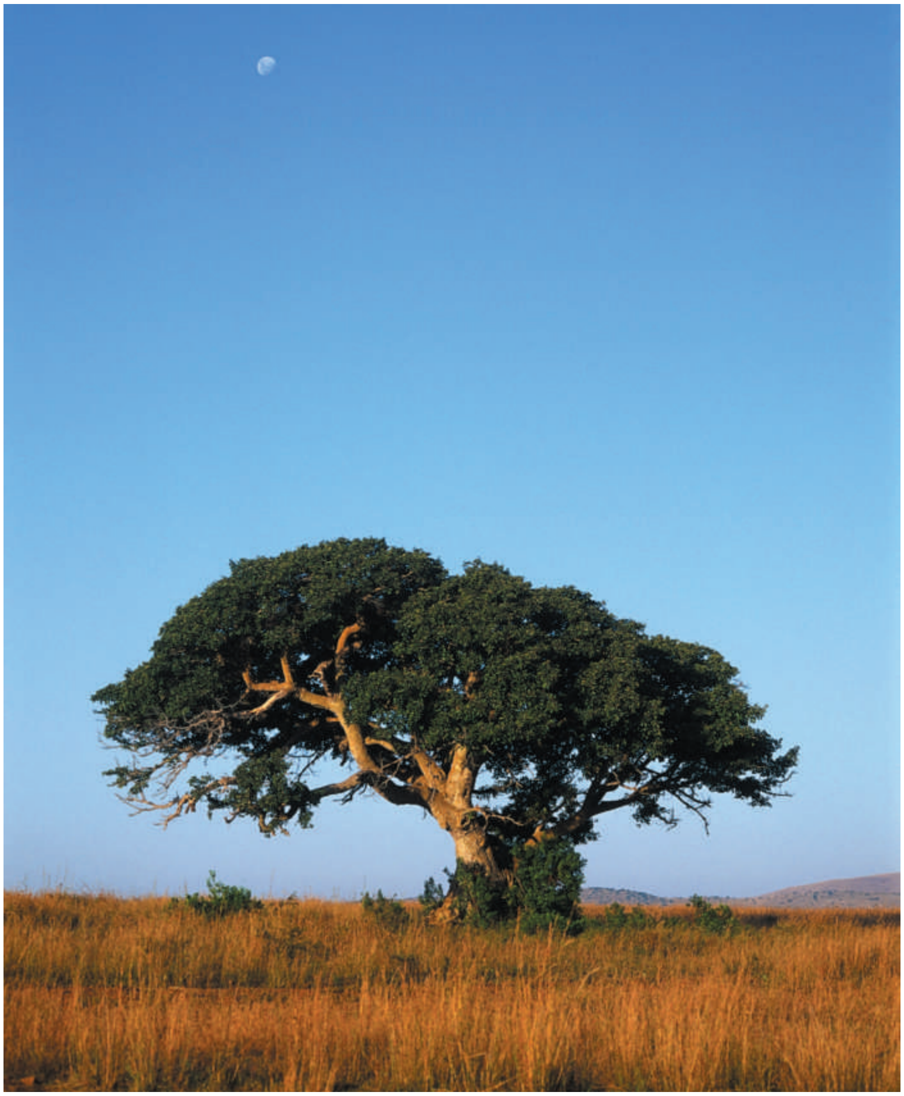
The extensive savannas of Africa, South America (locally known as cerrado) and Australia are primarily a result of either the climate or unique soil characteristics. Climatically derived savannas are warm all year but have distinct wet and dry (winter) seasons with annual rainfall varying widely from 30 to more than 100 centimeters of rainfall. What is critical about these climates is that during the dry season, rainfall amounts are very low. It is during these dry periods that the grasses are **dormant** and the trees experience water stress. Fires are also common at this time because the fine, dry fuel (dead foliage) that the grasses produce is very flammable. This allows fires, started by lightning or humans, to start easily and spread quickly. This combination of water stress and fire keeps the tree density low and distinguishes savanna from the adjacent forest.

dormant inactive, not growing

Other savannas occur in areas where there are unique soil conditions. Although most tropical and subtropical savanna soils are poor in nutrients, some also have a hard crust or barrier at some depth in the soil. This crust separates the shallow soil layer that the grasses rely on for water, and which dries during periods of low rainfall, from the deeper soil layers that may retain moisture all year. Trees in these savannas are located where cracks in the crust occur. In these places the roots of trees can access this deep soil water. Such savannas are referred to as edaphic (related to the soil) savannas.

Savannas as Transitional Zones

Savannas in both tropical and temperate zones may occur along the edge of forests where the dominant vegetation shifts from trees to grasses. This tension zone (also called an ecotone) between forest and grassland may be relatively narrow or 50 to more than 100 kilometers wide. These savannas usually occur where annual rainfall is not quite high enough to support a closed forest and where fire is common. In North America, the aspen parkland of Canada is an example of a temperate savanna and in the United States there are the oak savannas that extend from Minnesota to Texas. His-



A baobab tree on the African savanna.

torically, the region occupied by oak savanna moved eastward in periods of aridity and with frequent fire. In contrast, with fire suppression these savannas may be converted to closed canopy forest. Much of the original extent of North American savanna was found on deep fertile soils, but greater than 99 percent has been lost because the land was so valuable for row crop agriculture.

Savannas and Biodiversity

Savannas contain a mixture of forest and grassland species, as well as some species unique to this ecosystem type. Because of this they are important zones of high **biodiversity** for both plants and animals. In North America, oak trees embedded in tallgrass prairie vegetation are joined by species specifically adapted to partial shade and frequent fire. In Africa and Australia, thorny acacia, eucalyptus, and baobab trees are scattered among the grasses. Savanna grasses are well adapted to fire because their buds are protected below ground. Like the grasses, some mature savanna tree species are resistant to fire, particularly compared to other forest species. Many savanna trees (such as the oaks) have thick insulating bark that protects the

biodiversity degree of variety of life

Zebras on the savanna in Masai Mara, Kenya.

inner growing layers of the tree from fire. Others, such as the baobab tree in Africa, can store tremendous amounts of water in their bark and trunk, protecting them from both fire and drought. Other savanna trees are capable of resprouting vigorously after fire. Despite these adaptations, frequent fire decreases the density of trees in most savannas, with tree seedlings especially susceptible to fire.

herbivore an organism that feeds on plant parts

population a group of organisms of a single species that exist in the same region and interbreed

biomass the total dry weight of an organism or group of organisms

Savannas support a diverse array of **herbivores**, especially so in the African savannas. Grassland grazers such as zebras and wildebeest are found with herbivores that feed on trees, such as giraffes and elephants. Elephants have been termed a keystone species of African savannas for the role they play in determining the density of trees. When elephant **populations** are low, acacia trees and shrubs may become so dense that the grasses are shaded out and grassland species disappear. Conversely, if elephant populations are too high, the trees may disappear along with those species that depend on woody plants for food and shelter. Another group of organisms that is particularly notable in tropical savannas for their diversity and numbers, if not their individual size, are the termites. Conspicuous above-ground termite mounds are present in Australian and African savannas, but most termites live underground without building mounds. Termites fill a very important role as one of the major decomposers in savannas. As much as 90 percent of the grass **biomass** that is decomposed in some savannas can be attributed to termites. Thus, these organisms are valuable for making nutrients available to plants.

Savanna Management and Conservation

Most of the larger savannas in tropical and subtropical regions are grazed by livestock. Fire is used as a management tool to keep the density of trees low and stimulate the productivity of the grasses. Savannas can produce abundant plant biomass for grazers in regions with high rainfall, but savannas in the driest regions and with the most nutrient-poor soils can support only a modest number of livestock. In Africa, human-induced shifts in the populations of large native herbivores (elephants) have altered the density of trees in some savannas, and conservation programs for these species must also take into account their effect on other species as well as the savanna vegetation.

Interest in conserving and restoring savanna ecosystems is also great in North America, where the greatest proportion of the original savanna ecosystems has been lost. Controlled fire and even mechanical removal of woody species is typically used in areas where dense shrubs and tree seedlings have displaced the grasses. SEE ALSO BIOME; FABACEAE; GRASSES; GRASSLANDS.

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Seed Dispersal

Seed dispersal refers to the processes by which mature seeds disperse from the parent plant. Dispersal decreases competition with the parent and increases the likelihood of finding a suitable environment for growth. Sexual reproduction generally results in the production of fruits whose sole purpose is to enable the species to disperse and multiply. The part of the plant that acts in the dispersal is the diaspore (a term incorporating both fruit and seed). Although diaspore dispersal is the obvious end of reproduction, some plants rarely flower or set fruit and instead have evolved a very efficient system of vegetative reproduction by means of sucker shoots. Vegetative reproduction is very common in herbaceous plants that may spread by **stolons**, **bulbils**, or stem suckering. Still, most plants that reproduce vegetatively also reproduce sexually since this enables them to remain genetically variable and more adaptable to changes in the environment.

stolons underground stems that may form new individuals by sprouting

bulbil a small aboveground bulb

Wind Dispersal

The simplest form of seed dispersal is by wind and, not surprisingly, wind-dispersed fruits in temperate areas usually develop in breezy spring months. The same species that are wind-pollinated in temperate areas often bear wind-dispersed seed such as maple (*Acer* in Aceraceae), willow and poplar (*Salix* and *Populus* in Salicaceae), and ash (*Fraxinus* in Oleaceae).

A pisonia plant's seed clings to the feathers of a black noddy on Heron Island, Australia.

samara a winged seed

morphological related to shape

Typically the wind-dispersed seeds are developed quickly and dispersed in the same season. Wind-dispersed tree species are numerous in the warm, moist forests of the tropics—especially for tall trees in areas where there is a slight to prominent dry season. The height of the tree is important to enable the diaspore to catch the wind currents. The shape of wind-dispersed diaspores is often critical to their dispersal as well. Maple seeds have a **samara** and set up a whirling pattern as they fall, which may assist them in implantation. Poplar and willow seed are borne in a loose, cottony mass, which is extremely buoyant even in weak air currents. Although different **morphological** structures have evolved to disperse tree seed, the most common form of seed dispersal is wind-dispersed.

Typically, wind-dispersed species in tropical areas with seasonally dry periods lose their fruits late in the dry season or in the early rainy season that follows. This ensures adequate moisture for germinating seeds and adequate establishment before the next dry season. Wind-dispersed seeds have the distinct disadvantage of being at the peril of the elements. Most do not get carried very far away from the mother plant, and the population of insects that feed on the particular plant increases greatly at the time of flowering and can often destroy much of the crop. Some tropical species successfully avoid this by fruiting irregularly or even by what is known as mass fruiting, in which hundreds of individuals somehow manage to flower all at one time, literally swamping the predator population with more food than it can eat and thus preventing the insects from eating all the fruit.

The manner in which wind-dispersed diaspores are released is often critical to their dispersal. Because wet seeds do not float well on the air, most do not disperse except when the capsule is dry. Seeds are often contained within the capsule walls, and the valves of the capsule open increasingly further with only the uppermost seeds being capable of being blown free.

The same capsules may release seeds not from wind alone, but in part by mechanical motions and the inertia built up by movements of animals passing through a population. Each time a plant is bumped more seeds are cast away from it. This is a short distance but common type of seed dispersal in many prairie and forest edge plant populations.

Animal Dispersal

Animal-dispersed fruits are more common than wind-dispersed fruits and occur in species with a wider variety of life forms, including herbs, many vines, a modest number of tropical lianas, and shrubs as well as some trees. The morphology of animal-dispersed fruits varies depending on the organism doing the dispersal. The animals vary from those as small as ants to as large as horses or elephants.

Both birds and mammals are very effective dispersers. Birds are particularly effective dispersers since they can move the diaspore the farthest and the fastest. Diaspores dispersed by birds are usually colorful and lack any obvious scent (birds have keen vision but a poor sense of smell). Often the fruits feature contrasting colors so they are more easily seen. Frequently the outer covering of such fruit might be green or brown, but when the fruit opens the inner surface is bright red with a black seed. Often birds eat only the sweet portion of the diaspore and spit out the seed. If eaten, most seeds pass rather quickly through the bird's system and are ejected. Many times tiny colorful berries, such as those of *Anthurium* (Araceae), are initially quite sweet but quickly turn bitter after being eaten to encourage rejection. *Anthurium* also produces seeds with a sticky **appendage** that causes the seeds to stick to the bird's bill.

appendages parts that are attached to a central stalk or axis

Mammal dispersers are common in both temperate and tropical areas. Mammal-dispersed diaspores are usually not particularly colorful but may be tasty and even have a distinct aroma when mature. (Mammals have only average sight compared to birds but typically have a good sense of smell.) Squirrels and rodents in temperate regions gather and hoard oak and hickory fruits while tropical agoutis "scatter hoard" fruits by burying them seemingly at random on the forest floor. Those fruits that are not found later in the late rainy season—when fruit is rare—are already planted and ready to grow. Monkeys in the tropics have a diverse diet with a broad array of fruits that are dispersed by them. They are amazingly adept at dispersal, but seemingly wasteful since they gather many fruits, eat part of them, and then discard the remainder along with the seeds. Some less common animal dispersers are horses, which are known to eat and disperse the seeds of calabash (*Cresentia cujete* in Bignoniaceae) in Central America.

In the case of epizoochorous fruits, animals are responsible for dispersing fruits without actually consuming them. These are diaspores that attach themselves to fur or clothing. Among the most effective types are beggar's ticks (*Bidens* in Asteraceae), tick-trefoil (*Desmodium* in Fabaceae), and Queen Anne's lace (*Daucus carota* in Apiaceae). These fruits are difficult to avoid and are difficult to remove, so they are usually picked off and discarded far from where they were first encountered.

Mechanical Dispersal

legumes beans and other members of the Fabaceae family

lateral to the side of

Mechanically dispersed seeds are common in both temperate and tropical areas. Many **legumes** (Fabaceae) have fruits that dry under torsion, and are suddenly released when the two halves of the fruits fall apart. In this instant the two halves of the valve twist **laterally** and sometimes also longitudinally, which causes the dry seeds along their length to be thrown for considerable distances. One of the most remarkable mechanically dispersed seeds is that of *Hura crepitans* (Euphorbiaceae), which is made up of a series of pie-shaped segments that burst open with such force that it sounds like a rifle shot. Its small flat seeds are carried for great distances.

Water Dispersal

Water dispersal is quite effective in estuarian populations of plants. The nature of water-dispersed fruits is important since a seed that lacks buoyancy would sink to the bottom near the mother plant and have to compete with it. A diaspore that was too buoyant would perhaps never sink at all and thus might never be implanted. *Urospatha*, a tropical aroid, has fruits with seeds that are embedded in a thick, buoyant, gelatinous mass, which allows them to float for a period and then sink into the water. The seeds of some tropical trees that occur along water courses are known to be consumed by fish. It is not yet known, however, whether the movement of the fish are important to the dispersal of the seeds.

Seed germination and the establishment of the young plant is, of course, the only true sign of reproductive success. Dispersal without establishment is to no avail. In every case the rate of germination is critical. Many diaspores do not fall into the proper situation for germination. Often large numbers of seeds are killed by a wide variety of beetles or weevils that specialize on seeds. Different species have developed various methods of survival. Some, such as orchids, produce thousands of minute seeds per capsule, giving some a good chance of success. Other species use the opposite strategy of producing large and heavy fruits with a lot of stored food material to ensure survival after germination. Some species, such as the seeds of the *Beilschmiedia* in the Lauraceae, have an increased chance of survival by having the seeds begin the germination process while still on the trees, where they are less susceptible to attacks. The red mangrove *Rhizophora mangle* (Rhizophoraceae) goes even further by actually establishing a young plant on the tree that has a pointed base that actually implants in the soil when it falls. SEE ALSO GERMINATION; INTERACTIONS, PLANT-VERTEBRATE; SEEDS.

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Seedless Vascular Plants

The Lycophyta, Equisetophyta, and Psilophyta are collectively referred to as the fern allies because, like the ferns (Pterophyta), they reproduce by single-celled spores released from sporangia (spore sacs). They do not produce flowers or seeds and both ferns and fern allies contain well-developed conducting tissues to transport fluids within the plant. Fern allies, however, differ greatly in appearance from ferns because they generally bear small, simple leaves with an unbranched vein, whereas almost all ferns have larger, often lacy cut leaves called fronds that contain branching veins. The fern allies include some of the earliest known land plants, many of which are long extinct. Today, there are probably fewer species of fern allies than there were many millions of years ago.

The life cycles of the fern allies and ferns are similar. Alternating generations of sporophytes (**diploid** plants producing spores) live independently of gametophytes (**haploid** plants producing eggs and sperm). The **sporophyte** is the dominant of the two generations; it has two sets of chromosomes per cell and is larger and more conspicuous. Through meiosis in the sporangia (spore sacs), the number of chromosomes in some cells is reduced by half; these cells develop into spores. If a spore lands on a suitable site it will germinate to form a gametophyte, usually less than 1 centimeter across. The resulting gametophyte, with a single set of chromosomes per cell, produces an egg in each archegonium (vase-shaped structure) and sperm in each spherical antheridium. Sperm are released from antheridia and, in a drop of water, they swim to an egg and unite with it to create another sporophyte with two sets of chromosomes.

diploid having two sets of chromosomes, versus having one (haploid)

haploid having one set of chromosomes, versus having two (diploid)

sporophyte the diploid, spore-producing individual in the plant life cycle

Lycophyta

In the Carboniferous period (over three hundred million years ago), Lycophyta included large trees that are now extinct, but which have left remains preserved as coal. This division of fern allies is represented today by three distantly related families of small herbaceous plants called club mosses, spikemosses, and quillworts. The club mosses are homosporous (producing spores of one size) while spikemosses and quillworts are heterosporous (producing spores of two sizes). These plants generally grow to less than 20 centimeters high, rarely up to 1 meter. They have branched or unbranched stems that are erect, creeping, or hanging, and covered with simple, one-veined leaves. Their roots branch with equal forks. Sporangia are borne singly in the upper angle formed between leaf and stem. Leaves associated with sporangia are clustered in zones along the stem or packed into terminal cones. Heterosporous lycophytes are distinctive for the small flap of tissue on the upper surface of each leaf called a ligule.

Club Mosses (Lycopodiaceae). There are about 375 species of club mosses distributed worldwide, especially in mountainous tropical habitats. These large mosslike plants, whether terrestrial or epiphytic, have branching stems that are densely covered with small, narrow leaves. Unlike spikemosses and quillworts, club mosses are homosporous and have kidney-shaped sporangia that open like clams. The sporangia may be clustered in zones or packed in terminal cones. The small, disc- or carrot-shaped gametophytes associate with fungi for assistance with the uptake of nutrients. Princess pine (*lycopodium* sp) is a common lycopod in eastern forests.

Spikemosses (Selaginellaceae). Most of the approximately 750 species of spikemosses occur in tropical and subtropical regions where they occupy a variety of habitats ranging from rain forests to deserts. These mosslike terrestrial plants typically are less than 2 centimeters high. Like the club mosses, they have branching stems densely covered with small, narrow leaves. The sporangia of most species are packed in four-sided, terminal cones. They are heterosporous, usually producing four megaspores in each megasporangium and hundreds of microspores in each microsporangium. Upon germination, the tiny megagametophytes produce eggs and the minute microgametophytes release numerous sperm when the spore wall opens.

globose rounded and swollen; globe-shaped

Quillworts (Isoetaceae). There are probably over two hundred species of quillworts distributed worldwide in a range of habitats including lakes, streams, roadside ditches, and soil pockets on exposed rocks. The slender leaves of these terrestrial or aquatic plants can grow up to 50 centimeters long, and some can grow up to 1 meter. The short and squat to **globose** stems are covered with long, thin leaves, giving the plants the appearance of a tuft of grass. The sporangia are embedded in a basal cavity of the leaf. They are heterosporous, usually producing tens to hundreds of megaspores in each megasporangium and thousands of microspores in each microsporangium. Upon germination, the tiny megagametophytes produce eggs and the minute microgametophytes release four sperm when the spore wall opens.

Equisetophyta (Horsetails and Scouring Rushes)

whorls rings

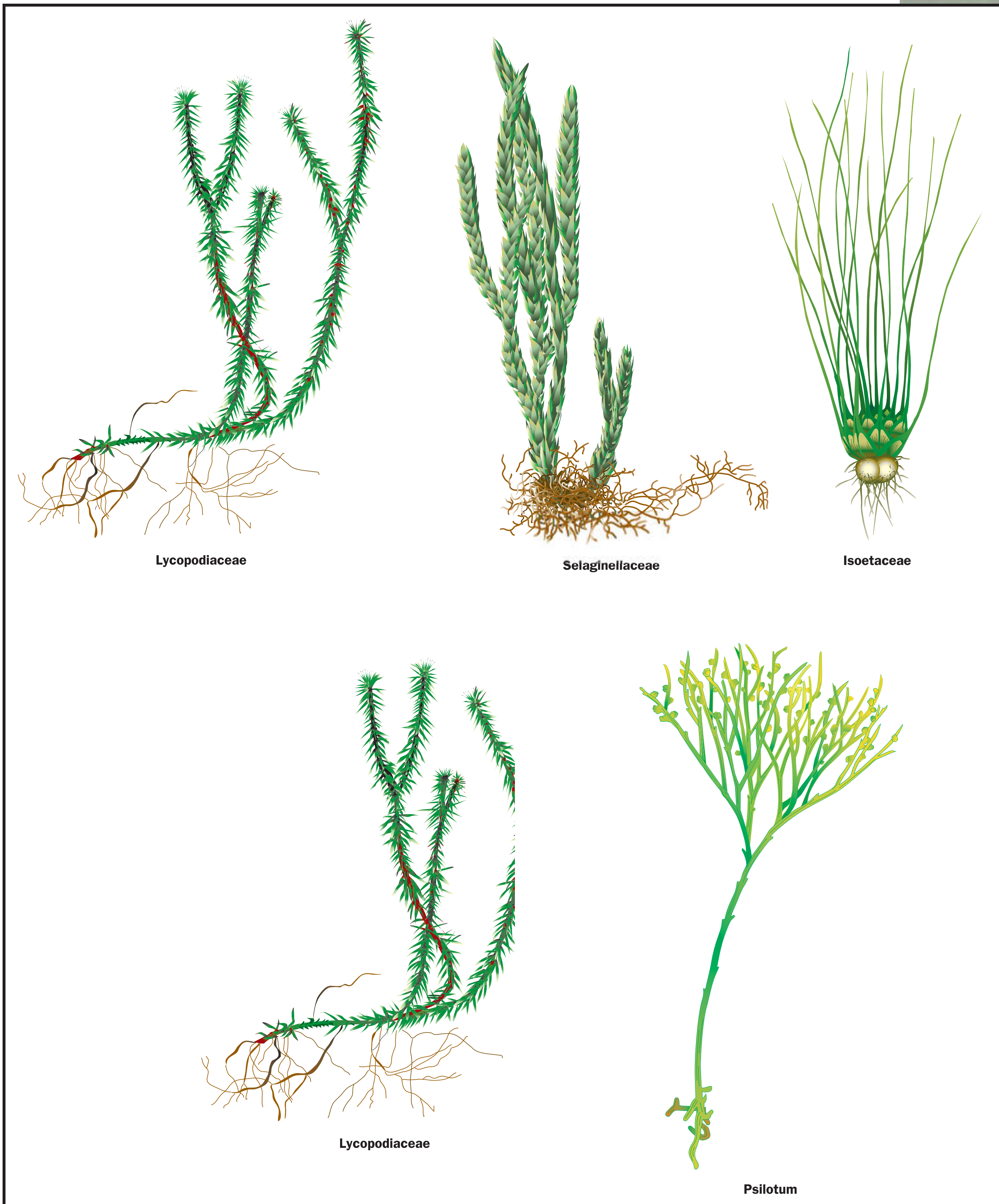
elater an elongated, thickened filament

These plants are distinctive for their tubular, grooved, and jointed stems. Although more diverse in the fossil record, today they are represented by only fifteen species, which are distributed nearly worldwide in moist to wet, often-disturbed habitats including shores, roadsides, marshes, and woodlands. Silica in the stems makes them useful for scouring and sanding—hence, one of their common names is "scouring rushes." These plants are usually less than 1 meter tall, but on occasion can grow to several meters. Their stems range from horizontal to erect and can be branched or unbranched. They bear **whorls** of leaves fused along their edges to form a slightly expanded sheath at each joint. In cross section, stems are seen to have a large central canal and smaller canals under the grooves and ridges. The sporangia hang from six-sided, umbrellalike sporangiophores, which are packed into terminal cones. The plants are homosporous and the spores are notable for the tiny, straplike **elaters** that coil and uncoil to aid in their dispersal. The small, lobed, cushionlike gametophytes initially produce either eggs or sperm. Gametophytes of some species, initially producing archegiona, later develop antheridia.

Psilophyta (Fork Ferns)

epiphytes plants that grow on other plants

The Psilophyta have long been thought to be among the most primitive of all living vascular plants because of their similarity in form to some of the oldest land plant fossils. Recent studies, however, indicate that they may be more closely related to the ferns than to the fern allies. There are about seventeen species, growing mainly in the tropics and subtropics. Most grow as **epiphytes** on tree fern trunks. They are called fork ferns (or whisk ferns) because the leaves associated with the sporangia (sporophylls) are forked, whereas their other leaves are simple or absent. Fork ferns grow less



Various types of seedless vascular plants.

than 0.5 meters high and are without roots. They have horizontal, erect, or hanging stems that may be branched or unbranched. Their leaves are scale-like and with or without a vein. They are homosporous, bearing two- or three-lobed, fused sporangia on or above the sporophylls. The spores produce small subterranean gametophytes that associate with fungi for assistance with the uptake of nutrients. Gametophytes look similar to the underground branches of the sporophyte. SEE ALSO BRYOPHYTES; EPIPHYTES; EVOLUTION OF PLANTS; FERNS; VASCULAR TISSUES.

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Seed Preservation

Conservation of crop genetic resources is important to the long-term health of the world's food production systems. Genetic diversity provides the raw materials for selecting and improving plant traits such as resistance to pests, diseases, and environmental stresses. Genetic engineering has greatly increased our ability to manipulate genes for the benefit of agriculture, including transferring genes between unlike species. However, until individual genes that code for a specific trait or set of traits can be designed and developed in the lab, researchers and plant breeders must rely on existing genes. Thus, saving and preserving seeds, and their genes, is critical to future food security and stability.

Providing access to a reservoir of plant genetic resources has been the goal of ex situ (outside of the place of origin or natural occurrence) conservation at both the national and international levels. Ex situ strategies include the storage of plant genetic resources in seed banks, clonal repositories, and living collections. An extensive system for the ex situ conservation of plant genetic resources has been developed in the United States under the auspices of the Agricultural Research Service (ARS), the main research agency of the USDA (United States Department of Agriculture). The National Plant Germplasm System (NPGS), established to preserve and promote the use of plant genetic diversity, is a collaborative effort between state, federal, and private entities to acquire and manage plant genetic resources, including wild and weedy crop relatives, **landraces**, obsolete cultivars, and elite lines or **populations** of agricultural, horticultural, industrial, and medicinal crops. Though the NPGS focuses on building a strong, competitive U.S. agricultural industry, all **germplasm** held in the NPGS collections is made available to researchers around the world upon request.

landrace a variety of a cultivated plant, occurring in a particular region

population a group of organisms of a single species that exist in the same region and interbreed

germplasm hereditary material, especially stored seed or other embryonic forms

Germplasm from all over the world is preserved in the NPGS system. Because many of the commercial crops produced in the United States are

Scientists at the Vavilov Plant Industry Institute in St. Petersburg, Russia, work with the seeds of such plants as drought-resistant wheat, barley, and corn. The institute is the storehouse of seeds gathered by geneticist N. I. Vavilov, who roamed Africa, Asia, and Latin America in the early twentieth century to establish one of the world's largest collections of genetic plant stock.

Structure of several species of seeds. Strictly, lettuce and wheat are not seeds, but fruits.

from nonnative sources, American agricultural productivity has depended on plant introductions from other countries, particularly from the tropics and subtropics. There are over four hundred thousand **accessions** from more than ten thousand species in the U.S. germplasm reserves. Responsibility for maintaining and distributing this large collection is divided between different NPGS sites, such as the eight National Germplasm Repositories, four Regional Plant Introduction Stations, the National Seed Storage Laboratory (NSSL), and other NPGS sites. Each site is charged with maintaining different species.

accession an individual sample of seed

The NSSL preserves the base collection of the NPGS and conducts research to develop new technologies for preserving seed and other types of plant germplasm. Seeds are stored either in conventional storage at -18°C or in cryogenic storage (liquid nitrogen) at -196°C. The National Germplasm Repositories are responsible for acquiring, preserving, increasing, evaluating, documenting, and distributing plant genetic resources of specific genera. United States germplasm collections of maize (corn), pumpkins, sunflowers, melons, cucumbers, and carrots are maintained at the North Central Regional Plant Introduction Station located in Ames, Iowa. The Western Regional Plant Introduction Station in Pullman, Washington, maintains lettuce, beet, bean, chickpea, forage and turf grass, and pea germplasm. Collections of pears, strawberries, blueberries, raspberries, and others are maintained at the National Clonal Germplasm Repository in Corvallis, Oregon, as living plants or, in the case of wild species, as seeds. Fruit and nut tree germplasm is maintained at the National Clonal Germplasm Repository in Davis, California.

Long-term storage of seed samples carries with it some inherent problems. The primary objective of seed banks is to maintain the genetic diversity and integrity of germplasm. Maintaining seeds in frozen storage requires adequate temperature and humidity controls. Even under ideal conditions, however, seeds eventually begin to lose viability—the ability to germinate.

NATIVE SEEDS/SEARCH

Native Seeds/SEARCH (NS/S) conserves the traditional seeds, crops, and farming methods that have sustained Native peoples in the southwestern United States and northwestern Mexico. Since 1983, the NS/S collection of crops and wild crop relatives has grown to nearly two thousand varieties of corn, beans, squash, amaranth, chilis, cotton, and other crops grown by Apache, Hopi, Maricopa, Mojave, Mountain Pima, Navajo, Paiute, Puebloan, Yoeme, and other farmers.

genotype the genetic makeup of an organism

Thus, periodically, new seed needs to be produced in order to replace aging seed samples. This process is referred to as regeneration. The loss of unique **genotypes** within a collection—whether from natural causes, small sample sizes, or random drift—nonetheless would constitute a change in the presence or frequency of genes within a germplasm collection.

During regeneration, plants are exposed to the risks inherent with agriculture—insects, diseases, drought, hail, temperature extremes, and wind, depending on whether they are grown under field or greenhouse conditions. When susceptible genotypes succumb to insect or disease pressures, the genetic variability and integrity of the collection may be compromised unless the genes lost are present in surviving genotypes. Thus, the need to regenerate a collection must be weighed against the need to minimize risks associated with regeneration. Additionally, genetic contamination through cross pollination or accidental mixing during post-harvest processes such as cleaning can also result in a loss of integrity.

Many small, independent organizations are also involved in seed saving. Together, they have created what is known as the heirloom seed movement. These organizations, groups, and individuals have helped bring about global awareness of genetic erosion—a reduction in the number of varieties, and, hence, genetic diversity—in commercially available vegetable and crop seed. Of the approximately five thousand heirloom varieties of vegetables available in the 1984 seed catalogs, 88 percent were no longer available by 1998. On average, there is a 6 percent loss in available varieties every year. Comparison of a USDA inventory of varieties available at the beginning of the twentieth century with a list of holdings in the NSSL at the end of the twentieth century revealed that only 3 percent of this germplasm survived in American germplasm reserves.

More than twenty-five small seed companies in the United States focus their efforts on slowing or preventing the loss of open-pollinated, heirloom seeds. Founded in 1975, Seed Savers Exchange collects, maintains, and distributes precious heirloom seeds through a network of eight thousand members. The vast collection of rare, heirloom seeds includes over eighteen thousand varieties of tomatoes, beans, peppers, squash, peas, lettuce, corn, melons, garlic, and watermelons from countries around the world. SEE ALSO Biodiversity; Cultivar; Native Crops; Seeds; Vavilov, N. I.

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Seeds

angiosperm a flowering plant

gymnosperm a major group of plants that includes the conifers

The seed is the dispersal stage of the life cycle of **angiosperms** and **gymnosperms**. It contains the embryo, the next generation of plant in miniature. Many seeds are dry when shed from their parent plant and are thus adapted to withstand harsh environments until conditions suitable for germination are achieved.

The evolution of plants to produce seeds is poorly understood because the fossil evidence is incomplete. The advantage of reproducing through seeds is apparent, however: The embryo is encased in a protective coat and is provided with a source of nutrients until, as a young seedling following germination, it becomes established as an independent photosynthetic (**autotrophic**) entity.

autotroph "self-feeder"; any organism that uses sunlight or chemical energy

Seeds account for 70 percent of food consumed by humans, and are also the major feeds for domestic animals. Their importance cannot be overstated. World seed production is dominated by the cereals, and even the production of wheat, maize, or rice alone by far exceeds that of all the other crops. As a concentrated source of carbohydrate, cereals provide for the human diet, livestock feed, and industrial raw materials. They are also an important source of protein, oil, vitamins, and fiber. Grain **legumes**, particularly soybeans and groundnuts (peanuts) are an important source of proteins and vegetable oils, which are used in margarine and cooking fats, and have applications in paints, varnishes, and plastics, as well as the manufacture of soaps and detergents. An understanding of seeds is therefore an essential prelude to human attempts to improve their quality and yield, whether it be by conventional breeding techniques or the novel approach of genetic engineering.

legumes beans and other members of the Fabaceae family

Seed Structure

A seed is a combination of maternal tissues, embryo tissues, and (in angiosperms) **endosperm** tissue. Seeds of different species are variable in size and internal structure at the time they are shed from their parent plant. They may be barely visible to the naked eye (for example, orchids), weigh a few micrograms to milligrams (for example, poppy, tobacco, and many annual weeds), weigh up to several hundred milligrams to grams (for example, soybean, maize, pea, and bean) or even several kilograms (coconut and *Lodoicea maldivica*).

endosperm the nutritive tissue in a seed, formed by fertilization of a diploid egg tissue by a sperm from pollen

Non-Maternal Tissues

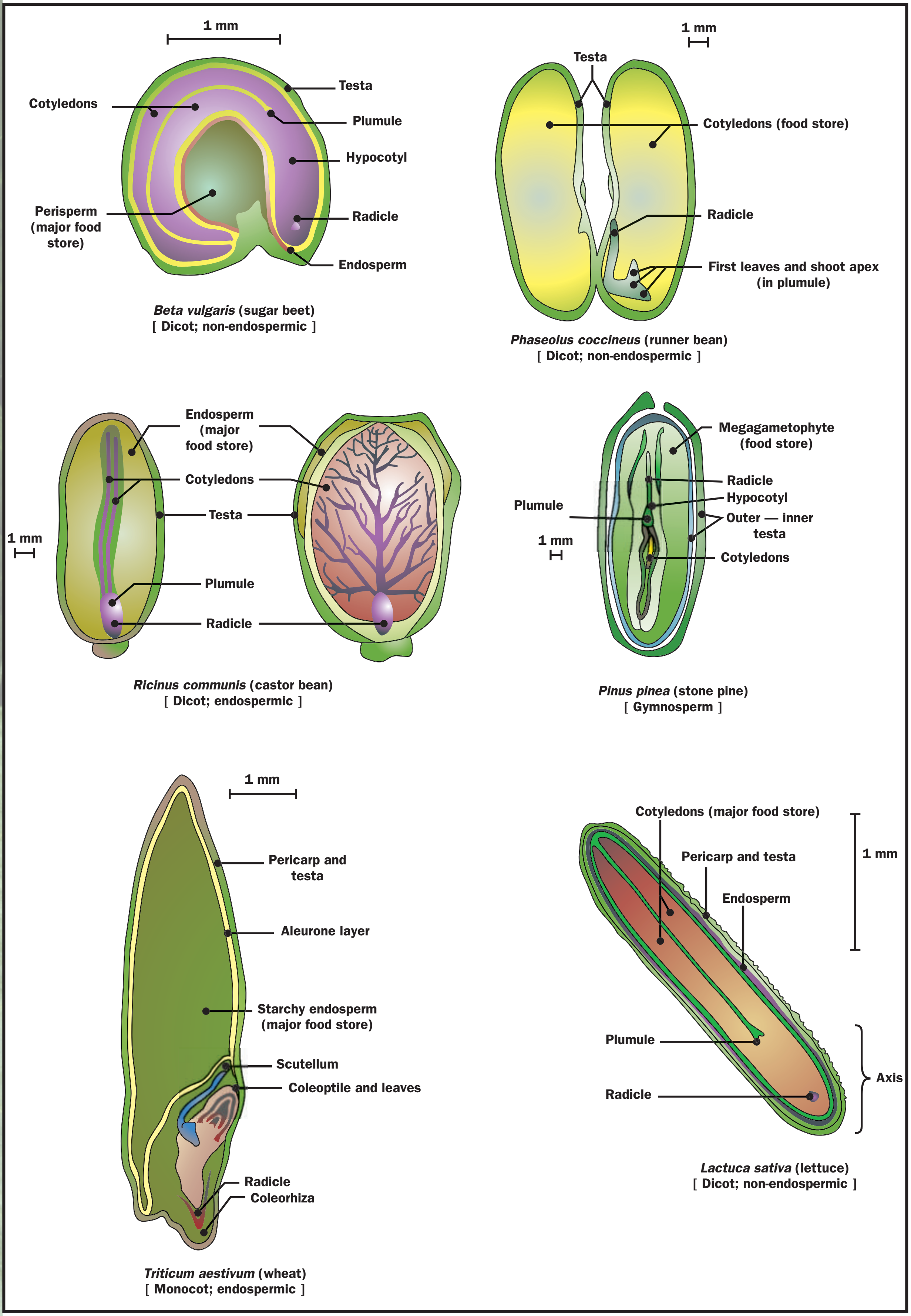
The seed develops from the ovule after the egg cell within has been fertilized by a male gamete from a germinated pollen grain. The resulting **diploid zygote** cell then undergoes extensive mitotic divisions to form the embryo. In angiosperms, the process of double-fertilization occurs when a second male gamete from the pollen tube fuses with two female nuclei in the ovule, yielding a triploid nucleus containing one set of paternal genes and two maternal sets. This also undergoes extensive mitotic divisions to produce the endosperm, usually a storage tissue that may (cereals, castor bean) or may not (peas, beans) persist in the mature seed, or it may be reduced to a thin layer of cells (lettuce, tomato, soybean).

diploid having two of each type of chromosome; twice the haploid number

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

Maternal Tissues

The seed coat (testa) develops from the outer layers of the ovule, the integuments, and is a diploid maternal tissue. In many angiosperm species the ovary wall surrounding the ovule also divides and develops at the same time as the seed to form an enclosing fruit. While many species form a fleshy fruit, in others the fruit tissues (pericarp) develop as only a few layers of cells,



Structure of several species of seeds. Strictly, lettuce and wheat are not seeds, but fruits.

become dry, and adhere to the outside of an equally thin or thinner seed coat. Strictly, by botanical definition, such dispersal structures are fruits (for example, cereal grains, lettuce, sunflower, oak). Nonetheless, for convenience, and because they contain the embryo, they are usually called seeds.

In some angiosperm seeds, following the completion of fertilization, another part of the ovule, the nucellar tissue, may divide mitotically and grow to produce a nutritive perisperm (sugar beet, coffee). In gymnosperm (conifer) seeds, the tissue surrounding the mature embryo is the megagametophyte, a **haploid** maternal tissue into which the fertilized zygote grows during seed development; it is still substantially present in the mature seed as a source of stored reserves.

haploid having one set of chromosomes, versus having two (diploid)

The Embryo

The embryo is made up of an axis bearing one or more cotyledons. The axial region contains a hypocotyl to which the cotyledons are attached, a radicle that will become the primary root following germination, and the plumule, the shoot axis bearing the first true leaves. These parts are usually easy to discern in dicot angiosperm seeds and in those of the polycotyledonous (many cotyledons) gymnosperms. But in seeds of monocot plants, particularly the cereal grains, the single cotyledon is much reduced and modified to form the scutellum, an absorptive structure that lies against the endosperm and absorbs material from it. The basal sheath of the cotyledon is elongated to form a **coleoptile**, which covers the first leaves.

coleoptile the growing tip of a monocot seedling

The shapes of the embryos and their position within the seed are variable between species. In those dicot species that have a substantial endosperm (endospermic seeds) the embryo occupies proportionately less of the seed than when the endosperm is rudimentary or absent (compare castor bean with lettuce or runner bean). In contrast, the cotyledons of nonendospermic seeds are much bulkier and are the storage tissues, and in peas and beans account for over 90 percent of the mass of the seed.

Several variations on this general theme occur. In the Brazil nut the cotyledons are much reduced and the bulk of the seed is occupied by a storage hypocotyl. Because the Brazil nut is primarily a single hypocotyl, it does not split in two like most other nuts made from two enlarged cotyledons. Cotyledons are absent from the seeds of many parasitic species. In orchids, seeds are shed when the embryos are extremely small and contain only a few cells, and completion of development occurs afterward.

Non-Embryonic Storage Tissues

In most species, the maternally derived perisperm fails to develop and is quickly absorbed by the developing embryo. Where it does persist, it is a major storage tissue, sometimes in conjunction with an endosperm, or the cotyledons (for example, sugar beet).

As noted, seeds are categorized as endospermic or nonendospermic in relation to the presence or absence of a well-formed endosperm within the mature seed. The relatively massive endosperm is the major source of stored seed reserves in species such as the cereals, castor bean, date palm, and endospermic legumes (carob, fenugreek). In the cereal grains and seeds of some endospermic legumes (for example, fenugreek) the storage cells of the endosperm are nonliving at maturity, and the cytoplasmic contents have been replaced entirely by the stored reserves (starch and protein in cereals; hemicellulose cell walls in fenugreek). But on the outside of the endosperm there remains a living tissue of one to a few cell layers in thickness, the aleurone layer, whose role is to synthesize and secrete **enzymes** to mobilize those reserves following germination.

enzyme a protein that controls a reaction in a cell

The Seed Coat (Testa)

The anatomy of the seed coat is highly variable, and differences among species have been used for taxonomic purposes. The coat is of considerable importance to the seed because it is a protective barrier between the embryo and the outside environment (in some species the fruit coat may augment or be a substitute for this role). Protection by the seed coat is aided by the presence of an inner and outer **cuticle**, impregnated with fats and waxes, and **lignified** cell walls. Phenolics or crystals (of calcium oxalate, for example) may be deposited in the coat to discourage **predation** by insects. Mucilage-containing cells may be present that burst on contact with water, retaining and absorbing moisture as a supply to the germinating embryo. Rarely, hairs or wings develop on the seed coat to aid dispersal (willow, lily); more frequently the dispersal structures are a modification of the surrounding fruit coat.

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

lignified composed of lignin, a tough and resistant plant compound

predation the act of preying upon; consuming for food

Quiescence and Dormancy

The completion of seed development and the acquisition of the mature structure is marked in many species by a loss of water, so that the mature seed can be dispersed in the dry state. The water content of a dry seed is usually 5 to 15 percent, versus 70 percent or more for the plant as a whole. When dry, a seed can withstand extremes of temperature that would rapidly result in death in the hydrated state. Not surprisingly, then, dry seeds are more or less in a state of suspended animation, with little or no metabolic activity. As such, they are said to be quiescent. When introduced to water again, under favorable conditions such seeds will rapidly resume metabolism and complete germination.

The phenomenon of seed quiescence is very different from that of dormancy. The latter is when seeds in a hydrated state fail to complete germination even when conditions are favorable; that is, temperature, water and oxygen supply are not limiting. **Dormant** seeds are metabolically active, in fact as active as their nondormant counterparts, but there exists within the seed a block (or blocks) that must be removed before germination can be completed. To be released from dormancy, a seed must experience a particular stimulus, or undergo certain metabolic changes. The cause of dormancy is not clearly understood, but at least one factor is the growth regulator hormone abscisic acid (ABA), which is imported from the parent plant into the seed during its development.

dormant inactive, not growing

Many seeds lose dormancy (while remaining quiescent) while still in the mature dry state, in a process called after-ripening, which may extend over several weeks to many years. Dormancy of hydrated seeds in the soil may be broken by one or more environmental cues, whose effectiveness depends on the species. These cues include: 1) light, usually for a short duration, with sunlight being the most effective; 2) low temperature, around 1 to 5°C for several to many weeks; 3) fluctuating temperatures, usually day-night

CONDITIONS THAT TERMINATE SEED DORMANCY

Species	Common Name	Light	Chilling	Alternating Temperatures	After-ripening
Acer pseudoplatanus	Great maple		+		+
Avena fatua	Wild oat		+		+
Betula pubescens	Birch	+	+		+
Hordeum species	Barley		+		+
Lactuca sativa	Lettuce	+	+		+
Nicotiana tabacum	Tobacco	+		+	
Pinus sylvestris	Scot's pine	+	+		
Prunus domestica	Plum		+		+
Triticum aestivum	Wheat		+		+

fluctuations of 5 to 10°C; and 4) chemicals, of which nitrate is the most important in the soil.

Dormancy is a mechanism to ensure the optimum distribution of seed germination in time and space. For example, seeds that require weeks of cold temperatures to break their dormancy cannot complete germination immediately after being shed from their parent plant in early fall, but will do so only following the cold winter months. This ensures that they are not in the delicate seedling stage at the onset of winter, which would be detrimental to their survival. Dormancy of light-requiring seeds will be removed only when seeds are at the soil surface, a mechanism that prevents germination at too great a depth. This is crucial for small seeds whose stored reserves are insufficient to support growth through the soil to carry the seedling leaves into the light to begin photosynthesis. Seeds on the forest floor receive light that is poor in the red wavelengths, since this is absorbed by the leaves of the overarching canopy. Thus, seeds in this environment must wait for the appearance of gaps in the canopy (tree fall or logging) before their dormancy can be broken, and they can then emerge in situations where there is reduced competition for resources from established plants. Phytochrome is the light-perception system in dormant seeds and is activated by wavelengths rich in red.

While the significance of dormancy can best be understood in an ecological context, it is important in agriculture too. Prolonged dormancy in crop species is undesirable since germination could be spread out over several years, resulting in unpredictable and low annual yields. On the other hand, lack of at least a temporary dormancy can be harmful also because, for example, mature seeds of barley or wheat could germinate on the ear if wetted by rain before harvest, resulting in crop spoilage. SEE ALSO EMBRYOGENESIS; FLOWERS; FRUITS; FRUITS, SEEDLESS; GERMINATION; GERMINATION AND GROWTH; GRAINS; PHYTOCHROME; POLLINATION; REPRODUCTION, FERTILIZATION AND; REPRODUCTION, SEXUAL; SEED DISPERSAL; SEED PRESERVATION.

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Senescence

Senescence refers to all of the many changes that inevitably lead to the death of part or all of a plant. Two related terms, *aging* and *longevity*, are also often used when senescence and eventual death are being discussed. Aging means all of the changes that occur over time, whether or not these changes lead to death, and longevity refers to how long a seed, or plant, or part of a plant, survives.

Senescence occurs in all plants and at all stages of the life cycle. Even in a young bean seedling, senescence processes have begun. The cotyledonary leaves, which were present in the dry seed, will rapidly give up their nutritive reserves to the growing plant, undergo senescence, and fall off.

tracheid a type of xylem cell for water transport

transpiration movement of water from soil to atmosphere through a plant

At the same time, root hairs and root cap cells are dying and being continuously replaced as the root grows. Elsewhere in the plant, cells are dividing, expanding, and differentiating. In the final stages of formation of vessels and **tracheids**, the living cell contents will undergo senescence and be removed. The remaining hollow tubes, consisting of just the cell walls, become the water-conducting pipes of the xylem tissues used in **transpiration**. Thus both whole-organ senescence (for example, a leaf, petal, or fruit) as well as specific-cell senescence, occur as a normal part of plant development.

pigments colored molecules

One of the visible symptoms of leaf senescence is the loss of the green chlorophyll **pigments** allowing the yellow carotenoid pigments to show through. In some maples (*Acer* spp.) in North America, red pigments, the anthocyanins, are made at this time. The senescence of leaves is triggered by environmental shifts (i.e., temperature and the relative lengths of night and day) and is also dramatically altered by applications of plant hormones. Cytokinins, auxins, and gibberellins can often delay senescence, while abscisic acid, ethylene, and jasmonates will accelerate these processes in some species. Some plants (for example, annuals like wheat, or perennial, deciduous maple trees that drop their leaves) have highly synchronous leaf senescence. In contrast, the bristlecone pine (*Pinus aristata*) may keep individual needles for up to thirty years. Among other plant structures, petals often undergo rapid senescence after the flower has been pollinated, and the final part of the ripening and softening processes in fruits is also a form of senescence. The manipulation of these processes—from the vase-life of cut flowers to the shelf-life of tomatoes—will remain an important economic target.

Underlying many, and perhaps all, of these diverse, visible patterns of senescence is an ordered sequence of gene expression, called programmed cell death, which is triggered either by environmental shifts or by internal mechanisms in the plant. By mutating, eliminating, or altering the expression of these genes, the pattern of senescence can be changed. A full understanding of these genetic processes, and their linkage to the environmental, hormonal, and time-dependent expressions of senescence in specific cells, tissues, and organs, will provide a new view of death in the plant kingdom. SEE ALSO Deciduous Plants; Genetic Mechanisms and Development; Hormonal Control and Development; Hormones.

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Sequoia

Sequoia is a genus of conifer containing one species, *Sequoia sempervirens*, the coast redwood. It is named for a Georgian Indian chieftain who invented the Cherokee alphabet. Traditionally included in the Taxodiaceae, current workers combine this family with the cypress family, Cupressaceae. One of the world's tallest tree species, sequoias can exceed 115 meters (360 feet) in height. The trunk, covered in red, shredding bark, is about 3 to 5 meters (10 to 16 feet) in diameter, but may reach 10 meters (33 feet). The branches bear both triangular and needlelike leaves. Male (pollen-producing) and female (seed-bearing) cones are borne on the same tree, but on different branches. *Sequoiadendron giganteum*, the giant redwood, formerly included in *Sequoia*, was placed in its own genus in 1939.

Coast redwoods form coniferous forests in western North America, from coastal central California to southernmost Oregon. Here they receive fog that provides moisture and cool conditions during the dry summer months. Coast redwoods are relics, plants that had wider distribution in the milder, moister climate of the past. Adult trees can live 2,200 years, and their thick bark resists most fires, which clear the undergrowth and create the open conditions needed for seedling establishment.

Redwood lumber is greatly desired, as it is rot resistant and straight grained. Therefore, redwood trees have been logged heavily during the last 150 years. Trees readily resprout from roots and stumps, so forests grow back quickly. Nevertheless, concern for the disappearance of virgin groves

A man stands besides a fallen redwood tree in California's Prairie Creek Redwoods State Park.

prompted the creation of Muir Woods National Monument in 1908. Less than five percent of the ancient redwood forests are intact, and most of those survive only through the protection of parks and National Forests. SEE ALSO Coniferous Forests; Conifers; Gymnosperms; Record-holding Plants; Trees.

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Shape and Form of Plants

Plants exhibit an enormous range of shape and form. Common shapes include the conical form of conifers, the vase shape of many shrubs, the linearity of scrambling vines, and the clumped form of a daylily. Ferns have a range of forms nearly as great as flowering plants, while mosses usually take the form of miniature herbs. These plant forms result from enhanced growth in one region occurring at the expense of growth in another area. Shape results from differential growth, localized cell division, and cell expansion.

apical meristem region of dividing cells at the tips of growing plants

New plant cells come from single embryonic cells or groups of embryonic cells called meristems. Two groups of embryonic cells are responsible for the origin of all new shoot parts in seed plants: the shoot **apical meristems** and the lateral meristems. Shoot apical meristems, also called primary meristems or growing points, are found at the tips of all stems. Cells from these meristems grow primarily by elongation. The meristems may be active simultaneously, with the apical meristems of branches increasing branch length while the apical meristem of the main stem increasing plant height.

The lateral meristems, which are also called secondary meristems, produce the secondary growth or the widening of plant stems. The two lateral meristems (the vascular cambium and the cork cambium) increase the diameter of the stem. The vascular cambium is a continuous circle of cells in

Branching in Japanese maples produces trees with a broad crown but a less regular form.

the stem interior and when active produces the woody portions of the stem. The cork cambium, also a continuous circle of cells, lies near the stem surface and when active produces the outer bark region. The activity of the lateral meristems is responsible for the increasing girth of plants as they age. Lateral meristems are active in plant regions where primary growth has ceased. Although increases in stem girth are associated with perennial plants, lateral meristems are also active in some annual plants (e.g., soybean) and increase their girth during the season.

Contribution of the Stem

Stems contribute to overall form in five major ways: growth direction, diameter, length between leaves, branches, and branch location.

Growth Direction. Stems are upright in most plants (such as corn or oak), growing away from gravity, but may be prostrate, as in creeping plants (e.g., creeping devil cactus), which grow at right angles to or without respect to gravity. Creeping stems of pot-grown plants may grow beyond the pot edge, down the side of the pot, and across the table the pot is on. This type of stem growth is contact dependent. The stems are not weak, but often quite stout. Stems of other shoots are lax (e.g., ivy), unable to support themselves, and their direction of growth is related to the availability of a host plant or a **substrate** to provide support.

substrate the physical structure to which an organism attaches

The number, location, and growth angle of the branches regulate tree form. Stems growing in different orientations are frequently found on the same plant. Christmas trees (fir or spruce, usually) have a main stem, which grows upright, and many side stems (branches) that grow at a regular angle to the stem. Many branches grow out at the same location and their orientation with respect to the stem yields a highly symmetrical, regular tree. On the other hand, branching in oaks and maples produces trees with a broad crown but a less regular form. Herbaceous plants exhibit the same features, although they are not as obvious as in conifers or large trees. The branches in these examples duplicate the architecture of the main stem, sometimes with great precision, to provide additional surface area for continued vegetative growth. Profuse branching in one plant shades out neighbor plants and limits their ability to compete for sunlight.

Branches may also be specialized for propagation and for reproduction rather than photosynthetic activity. Herbaceous plants such as strawberries have a main stem with only a few branches. Each branch extends far from the parent plant but finally touches the ground to establish a new plant. The new plant becomes independent of the parent and the linking stem can be severed with no harm to the new plant. These branches are called runners or stolons. Runners do not change the form of the parent plant, but instead duplicate the entire plant at a nearby location. The length of the runner prevents both plants from competing for the same resources, and the strategy is an effective means of vegetative propagation.

Reproduction often triggers change in plant form, commonly by enormous extension of the main axis, which might be topped by a single flower (e.g., iris, amaryllis, spring bulbs). Flowering in other species results in the outgrowth of branches from the main axis; reproductive branches may perfectly replicate or produce a slight modification of the pattern of flowers on the main stem.

Stem Diameter. Stem diameter may be the same along its entire length, either narrow (many annuals) or broad (palms). Other plants have conical stems (the main stem of a woody perennial), which result from secondary growth occurring at the base of the stem, while primary growth occurs at the top of the stem. With each new season of growth the stem base broadens. Lastly, stems may have an obconate form (upside-down cone), broader at the top than the base. Such a stem is inherently unstable and two conditions are common. In corn, the stem has roots that grow out from lower leaf positions. These stem-borne roots act as guide wires to stabilize the plant. In other species, secondary growth from an active vascular cambium stabilizes the plant and masks the obconate form.

whorls rings

internode the distance on the stem between leaves

Length Between Leaves. The stem length between adjacent leaves, leaf pairs, or **whorls** of leaves varies. When it is very short, a rosette plant is produced (e.g., strawberry, lettuce, ferns) that hugs the ground with a tight cluster of leaves. Tree ferns and palms have aerial rosettes, a series of closely spaced leaves produced each growing season. The stem is exposed as the old leaves die and fall, leaving a clump of green leaves at the top of the stem. Neither of these plants grows quickly, so tall tree ferns and palms are often more than one hundred years old. At the other extreme is papyrus, which bears a single **internode** topped by a cluster of leaves and associated floral branches. Sweet woodruff, a common garden plant, has stems with what appear to be whorls of leaves clustered at a single point on the stem followed by a substantial internode. When studied carefully, the whorl is a spiral of leaves with very short internodes, but a long internode separates each pseudowhorl of leaves. This is an obvious example of how differential growth yields variation in plant form.

Plants often have internodes of different length along the stem. A common pattern is short internodes at the base followed by long internodes and topped by short internodes. The diameter of these internodes changes as well, with short basal internodes having a greater diameter than the short internodes at the top. Again, differential growth regulates plant form. There may be a structural advantage to this organization: the short broad internodes at the bottom supporting a tall stem with short terminal internodes in the reproductive region. This organization would be advantageous in flower display to pollinators and in pollen dissemination by the wind.

Vines display an entirely different growth that is linked to their life strategy. In these plants, the internodes are long, even near the shoot tip, and leaf growth is limited. However, once the vine has made contact with a support, then leaf growth occurs. Vines put their energy into extending the stem into the light and attaching themselves to the substrate, and then the leaves expand.

axil the angle or crotch where a leaf stalk meets the stem

Branches and Branch Location. A branch develops from a bud located where the leaf joins the stem (the **axil**). Each bud has growth potential, but some buds never grow out and sometimes only buds in particular locations extend. Differential growth of the shoot apical meristems regulates overall plant form. If the buds do not develop, the stem remains unbranched. In some instances, the terminal apical meristem prevents the outgrowth of lateral buds, but the buds grow out if the meristem is removed or damaged. Gardeners often remove the main shoot apical meristem so new buds will grow out and ultimately produce more flowers. On some plant species (such as chrysanthemum), meristem removal takes place several times during the season to create a bushy plant covered with flowers.

In other species, only buds located at the base of the stem extend as branches, which results in a shrub that with each succeeding season grows more dense. In yet other plants, like the conifers, buds at a particular location (produced near the beginning or end of a growing season) will expand to give the plant a tiered appearance. Thus, the lower tiers have longer branches than those near the top because they have grown for more seasons. This gives the Christmas tree its conical shape.

Some trees take on a candelabra appearance (e.g., buckthorn, lilac) because the apical meristem on the main axis dies at the end of the year and two or more branches grow out in its place. In the following year, the apical meristem of each branch dies and two new branches grow out in place of the old one. The death and replacement strategy creates plants with highly regular forms. The same strategy is found in *Philodendron* and *Anthurium*, common houseplants, and many orchids, although it is less obvious in these species because only a single replacement branch grows out and subsequent plant growth obscures the branching pattern. The horsechestnut (*Aesculus*) also has single replacement branches.

Contribution of the Leaf

Leaves contribute to overall plant form through their size, shape, and arrangement around the stem. Leaves consist of two or three parts. Corn and leek leaves have two parts, a basal ensheathing portion and a long blade region. Geranium and oak leaves have three parts, a base region, a stalk called the petiole, and a terminal blade. The blade may be simple, an entire unit, or dissected, divided into several units called leaflets. The leaflets occur in two arrangements. When leaflets lie on opposite sides of a central axis and are terminated by a leaflet, the arrangement is featherlike or pinnate. When all leaflets are attached to the end of the petiole, the arrangement is fanlike or palmate (like the digits of a hand). Sometimes leaflets are attached around the entire circumference of the petiole, as in lupines, or the petiole is attached to the middle of the leaf blade, as in nasturtium.

Leaves are frequently similar in shape but differ in size. For example, leaves of banana and scallion or green onions are united by shape, as are those of feather palms and many common ferns. Leaves on a single plant may also differ in shape; sometimes shape change is dramatic and other times quite subtle. These changes may be related to the life history of the plant or result from a change in the direction of growth.

Leaves are present either in spirals (one leaf at each stem position) or in whorls (two or more leaves at each stem position). The most obvious spiral leaf arrangement is shown by *Costus*, a member of the ginger family, in which single leaves are arranged in an ascending spiral around the stem. Corn, which has leaves present in two vertical rows along the stem, also has a spiral arrangement. One can demonstrate a plant's spiral nature by winding a string from one leaf position to the next higher leaf position. In a few plants, a spiral of leaves will have little space between each leaf, making them appear whorled, and a large gap before the next spiral of leaves. These are

Pseudo-whorled leaf arrangements are found in select species of sweet woodruff, this common garden plant.

pseudo-whorled arrangements and found in select species of *Impatiens* and *Peperomia* and in a common garden plant, sweet woodruff.

The simplest form of whorled leaf arrangement is that of two leaves at a common stem position, seen in sunflowers, plants with opposite leaf arrangements. In members of the mint family, which includes garden mints and the common houseplant coleus, leaves originate in pairs, but each successive pair is offset 90 degrees from the previous pair. There are also plants with whorls of three leaves, such as oleander, where the succeeding set of leaves is offset from the preceding set. Looking down the length of the stem, there are six leaf positions, but only three positions are filled by each individual whorl. SEE ALSO ANATOMY OF PLANTS; MERISTEMS; PHYLLOTAXIS; TREE ARCHITECTURE.

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Soil, Chemistry of

The chemistry and fertility of soils have been of concern to humans since ancient times. One of the earliest books to correctly identify the soil as the source of plant mineral nutrients is *Organic Chemistry in its Application to Agriculture and Physiology*, authored by the German chemist Justus von Liebig (1803–1873) and published in 1840. Liebig's book was based, in part, on research conducted and reported in the 1820s and 1830s by German agronomist Carl Sprengel (1787–1859). Although this field still includes study of plant nutrients, modern research is also focused on the reactions and chemistry of pollutants such as mercury, arsenic, and organic pesticides in soils.

The sundew (*Drosera petiolaris*), found in Papua New Guinea and Indonesia, utilizes the sticky, shiny droplets on the end of its stem to trap small insects, which it digests to supplement the lack of nitrogen and phosphate in the soil.

Soil Components

The mineral fraction of soils is derived from rocks and minerals and composed largely of oxygen, silicon, and aluminum. After these elements, the most abundant in soil are iron, carbon, calcium, potassium, sodium, and magnesium. The organic fraction of soils is usually about 1 to 5 percent by weight; it forms during microbial decomposition of dead plant and animal material. Carbon, oxygen, and hydrogen are the major constituents of soil organic matter, which also contains nitrogen, phosphorus, and sulfur. Although plants do not directly absorb organic forms of nutrients, microbial processes can transform the nitrogen, phosphorus, and sulfur in soil organic matter into plant-available (inorganic) forms.

The chemical structure of clay minerals gives them charge; most have a net negative charge or a very low net charge close to zero. Negatively charged soils retain positively charged ions called cations (e.g., Mg^{2+}, Ca^{2+}). The total amount of negative charge in a soil is called cation exchange capacity (CEC). Some plant nutrients, such as calcium, magnesium, and potassium, are cations, and, therefore, soils with higher CEC values are able to retain more plant nutrients than those with lower CEC values. Organic matter has a higher CEC value than clay minerals and increases a soil's fertility.

Essential Elements for Plant Growth

An element is considered essential for plant growth when plants are unable to complete their life cycles without it. Sixteen to eighteen elements are recognized as essential including carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, sulfur, calcium, magnesium, iron, manganese, copper, zinc, boron, molybdenum, chlorine, and, for some plants, cobalt and nickel. Plant carbon comes from carbon dioxide in the atmosphere, and plant hydrogen and oxygen from water in soil. The other elements come primarily from the inorganic and organic fractions of soil. Macronutrients (nitrogen, phosphorus, potassium, sulfur, calcium, and magnesium) are needed by plants in relatively large quantities. Micronutrients, also called trace elements, are those elements usually contained in concentrations less than 100 milligrams/kilogram plant tissue (iron, manganese, copper, zinc, boron, molybdenum, chlorine, cobalt, and nickel).

PH LEVELS

pH is a measure of acidity (determined by hydrogen ions [H^+]) or alkalinity (determined by hydroxyl ions [OH^-]). In a pure water solution the concentration of hydrogen ions equals the concentration of hydroxyl ions at a value of 10^{-7} M (moles per liter). Such a solution of equal amounts of hydrogen and hydroxyl ions is said to be neutral and have a pH of 7. Acid solutions contain a higher concentration of hydrogen ions than of hydroxyl ions. Solution acidity is usually reported as the negative logarithm of the hydrogen ion concentration. So a solution with a hydrogen ion concentration of 10^{-4} moles per liter has a pH value of 4. In an aqueous solution, pH values less than 7 indicate an acid solution while pH values greater than 7 indicate an alkaline solution. In soils pH values generally range between about 4 and 10.

Importance of Soil pH

Soil **pH** is an important property that influences many chemical and biological processes occurring in soils. Acidification of soils is a natural geologic process. Rainwater contains carbonic acid produced when atmospheric carbon dioxide dissolves in the rain. In addition, plants may acidify the soil around their roots by releasing hydrogen ions. Human processes, such as combustion of fossil fuels, may add acidity to the atmosphere; this acidity eventually reaches soils via precipitation (acid rain) and deposition of dry particles. Although many soils have a large capacity to neutralize incoming acidity without changes in their pH values, over geologic time soil pH values decrease.

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral; low pH numbers indicate high acidity; high numbers indicate alkalinity

Soils in arid environments tend to have pH values above 7. The presence of soluble carbonates in these alkaline soils maintains high pH values. Soils containing high amounts of sodium carbonate can have pH values in the range of 8.5 to 10. These soils are called sodic and generally present severe limitations to plant growth. Alkaline and sodic soils may become neutral over time if exposed to enough precipitation to remove all the carbonates by dissolution and leaching. Neutral soils, which contain no carbonate minerals, tend to have pH values between 6.6 and 7.3 and are generally suitable for the growth of a wide range of plant species. Acid soils, which have pH values of 6.5 and below, tend to be found in regions with abundant rainfall and moderate to high temperatures.

One of the most important consequences of soil acidity is the dissolution of aluminum (Al^{3+}), which is toxic to plants, from soil minerals. Aluminum in soil solution interferes with both cell division and cell elongation and produces short, stubby root systems. Because of its strong positive charge, aluminum is strongly held on negative exchange sites, partially displacing calcium, potassium, and magnesium and reducing their availability. It may be difficult for plants to take up sufficient phosphorus when growing in acid soils because of chemical reactions between aluminum and phosphorus. Many micronutrients become more soluble at lower pH values, including manganese. Manganese is abundant enough to be toxic to plants in some low-pH soils. Lime (ground calcium and magnesium carbonate) is often added to acid soils to correct these problems and improve the soil environment for plant growth.

Effects of Excess Nutrients on Ecosystems

The nutrients most commonly limiting for plant growth in both terrestrial and aquatic systems are nitrogen and phosphorus. Both are often added as fertilizer to agricultural **ecosystems**. Nitrogen is generally readily soluble and leaches from soils to surface and ground waters. Phosphorus is strongly absorbed in most soils and typically reaches surface waters attached to particles eroded from agricultural fields. Both nutrients may promote excess algal growth in lakes and the ocean. When large quantities of algae grow, die, and are decomposed in the water, dissolved oxygen is depleted and aquatic organisms may die. Scientists have known since the 1960s

ecosystem an ecological community together with its environment

that nitrogen and phosphorus were negatively affecting some lakes and rivers. During the 1980s and 1990s dissolved oxygen levels declined in the Gulf of Mexico. By the late 1990s, a large area of the Gulf was almost devoid of aquatic life apparently due to nutrients transported by the Mississippi River. SEE ALSO AGRICULTURAL ECOSYSTEMS; ATMOSPHERE AND PLANTS; BIOCHEMICAL CYCLES; DECOMPOSERS; FERTILIZER; NITROGEN FIXATION; NUTRIENTS; SOIL, PHYSICAL CHARACTERISTICS OF.

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Soil, Physical Characteristics of

Soil physical properties are those related to the size and arrangement of solid particles, and how the movement of liquids and gases through soils is affected by the particles. Soil mineral particles are derived from the weathering of rocks and minerals. Soil organic matter is the product of microbial decomposition of the remains of plants and animals.

Soil Texture

Soil texture refers to a particular soil's distribution of mineral particles within certain size ranges. (Organic matter is removed before soil texture is determined.) Soil texture is an intrinsic property of a soil, which may be influenced by geologic processes such as erosion, but generally does not change appreciably within a human life span or as a result of human activities. Different groups use different classification schemes for particle sizes. A commonly used scheme is that of the U.S. Department of Agriculture (USDA). Although soil particles are rarely spherical, the USDA classification system is based on particle diameters.

Using the USDA classification system, gravel is between 2 and 75 millimeters, cobbles 75 to 254 millimeters, and stones greater than 254 millimeters. Soil is considered to consist of particles less than 2.0 millimeters in diameter. Sand-sized particles have diameters between 0.05 and 2 millimeters. The smallest sand particles are nearly invisible to the eye. Silt-sized particles range between 0.002 and 0.05 millimeter. Root hairs, nematodes, and fungi are also in this size range. Clay-sized particles are less than 0.002 millimeter in diameter. They are in the size range of bacteria and viruses.

In any soil analysis, the total amount of sand, silt, and clay in a soil always adds up to 100 percent. There are twelve soil textural classes defined by the percentages of these size groups. Along with an analysis of the percentages of sand, silt, and clay in a soil sample, a diagram called a soil textural triangle is used to determine a soil's textural class. For example, soils containing equal amounts of sand, silt, and clay are classified as clay loams. Although the term loam refers to a soil with a particular textural composition, loam is commonly used by nonsoil scientists to mean a fertile soil with a texture neither too sandy nor too clayey. Sandy soils are also called coarse-textured, clayey soils are referred to as fine-textured, and soils with a balance of sand, silt, and clay may be called medium-textured.

Soil Structure and Porosity

porosity openness

The arrangement of primary particles, particularly clays, into clumps or aggregates is referred to as soil structure. Soil organic matter is generally involved in binding particles into stable aggregates. The amount and arrangement of aggregates determines the total **porosity** of a soil. Total porosity of a soil can be determined from the soil's bulk density, the weight of a fixed volume of dried soil. The individual mineral particles in soil have

A U.S. Department of Agriculture researcher checks soil porosity using computer-enhanced images.

an average density of about 2.7 g/cm^3, and the organic matter has a much lower density in the range of 1.2 to 1.5 g/cm^3. A volume of dried soil contains mineral particles, organic matter, and pore space; although, of course, only the mineral and organic fraction contribute to the weight. The higher the bulk density, the lower the total pore space available for air and water within a soil. Soil bulk density ranges from about 0.1 to 0.7 g/cm^3 for highly organic soils and 0.9 to 1.8 for mineral soils. Sandy soils have higher bulk density values than those with more clay. Bulk density values higher than about 1.4 g/cm^3 indicate possible limitations to root growth and penetration; typical bulk densities for cultivated soils are 1.0 to 1.25 g/cm^3.

Porosity influences both gas diffusion and water movement in soil. As a generalization, a medium-textured soil with good aggregation contains about 50 percent pore space and 50 percent solid particles by volume. Porosity values can range from 25 percent in compacted soils to 60 percent in highly organic, well-aggregated soil. Macropores, also called aeration pores, are the larger pores between soil aggregates that allow relatively rapid water movement through a soil profile. More macropores in a soil means faster infiltration of water into the profile. Micropores are pores within aggregates; although they may represent a significant fraction of a soil's total porosity, water does not move rapidly through these small-diameter pores.

Porosity greatly influences water relations in soils. Soils with high clay content usually have a greater total porosity than sandy soils. However, a high percentage of the total pores are micropores that do not permit rapid water movement. Therefore water infiltrates slowly into, and out of, these high-clay soils. During a rain event, water may run off the surface of these soils more rapidly than it moves downward into them. Once they become wet, they dry out slowly. Sandy soils, with a higher percentage of macropores, have a high water infiltration rate. Water moves rapidly through the profile, and the soils generally dry out rapidly after rain.

Soil Tilth

Soil tilth, used more commonly by the general public than by soil scientists, is a general term for the physical condition of a soil. Soil tilth is influenced both by soil texture and soil structure. A soil with good tilth offers little resistance to penetration by plant roots during their growth. It also provides ample oxygen and water for plants. The presence of both macropores and micropores is important for good tilth. Macropores permit infiltration and drainage of water; micropores store water for future plant needs. Both the pore distribution and the amount of rainfall received influence whether the pores in any soil contain water or air. Capillarity refers to the ability of small pores to retain water against the force of gravity and results from the adhesive forces between water molecules and the particles in soil and from the cohesive forces between water molecules. Because small pores tend to be water-filled due to capillarity, fine-textured soils with little structure and large amounts of micropores may have inadequate oxygen for plant growth. Oxygen diffuses rapidly through air-filled pore space and slowly through water-filled pore space. Mechanized agricultural practices tend to destroy soil structure and compact soils, resulting in poor tilth. **Compaction** results from the pressure exerted on soils by heavy equipment moving over them. Agricultural practices also tend to destroy organic mat-

compaction compacting of soil, leading to loss of air spaces ter in soils that is needed to maintain structure. SEE ALSO AGRICULTURE, ORGANIC; COMPOST; DECOMPOSERS; PLANT COMMUNITY PROCESSES; ROOTS; SOIL, CHEMISTRY OF.

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Solanaceae

legumes beans and other members of the Fabaceae family

domesticate an organism adapted to live with and to be of use to humans

compound a substance formed from two or more elements

alkaloids bitter secondary plant compounds, often used for defense

physiology the biochemical processes carried out by an organism

Although not large, the Solanaceae, or Nightshade family, is certainly one of the most economically important plant families. It includes about 2,500 species in 90 genera. The potato/tomato genus, *Solanum*, includes about one-half of the species. Many place the family third in worldwide importance to people, behind the grasses and the **legumes**. This ranking is based on the many food and drug plants found in this genus. Virtually all of the edible plants were prehistoric **domesticates** of Latin America, except eggplant (from India). Among the species that had dramatic effects on world cuisine and history are potatoes, tomatoes, and hot (chili) peppers. Prior to 1492, there were no hot peppers in China or Southeast Asia, no tomatoes in Italy, no potatoes in Ireland or Russia, and no tobacco in Europe. In addition, several minor domesticates from the New World have had a lesser impact: tamarillo, tomatillos (the "ground cherries" of North America), and pepinos. Pepinos are eaten fresh, whereas the other two are usually eaten cooked; tomatillos together with chile peppers constitute the salsa verde popular in the Southwest United States.

The family is sometimes referred to as the paradoxical nightshades because it includes so many domesticates of such importance—the modified stems that constitute the tubers of potatoes follow only corn, wheat, and rice in production as world crops—and at the same time, so many toxic plants. Although the family's origin and greatest diversity are in Latin America, the Nightshades first became notorious in written history based on the toxic **compounds** of Mediterranean plants. The strong tropane **alkaloids** like atropine and scopolamine that make henbane, belladonna, and mandrake so poisonous are used in medicine today. Atropine is used to promote pupil dilation in ophthalmology (the wider pupils the drug promotes were taken advantage of by Italian women to make their eyes more attractive—hence the name, belladonna). However, the most significant drug plant in the family is tobacco, from the New World.

Belladonna, also known as deadly nightshade.

In addition to direct economic importance, various members have been significant in plant **physiology** (studies of day length and flowering), biotechnology, and molecular biology. The family includes a number of ornamentals, most prominently, *Petunia*, *Salpiglossis*, and *Brunfelsia*.

The herbs, shrubs, trees, and lianas (climbing vines) in the family grow in habitats from deserts to tropical forests, from sea level to the Andes Mountains. The leaves are generally alternate, petiolate, and simple, although they can be lobed or compound, and are often covered with hairs and sometimes with prickles (trichomes). The unusual vascular tissue has internal phloem. The flowers, solitary or in **inflorescences**, are usually radially symmetrical, **pentamerous**, and have a calyx and corolla united in short or long tubes. Thus, the corolla can be tubular, rotate, or **campanulate**. The mostly hermaphroditic flowers bear stamens attached to the corolla tube with anthers that break open to release pollen, by longitudinal slits, or by terminal pores in *Solanum*. The **gynoecium** consists of a single **pistil** and generally has a superior two-carpellate, two-locular ovary with numerous ovules. Except in *Solanum*, a floral nectary is often present at the base of the ovary. The fruit is mostly a juicy berry or a dry capsule, characteristically with the calyx persistent. Many species are pollinated by insects, although some are pollinated by hummingbirds, perching birds, or bats. SEE ALSO Potato; Potato Blight; Psychoactive Plants; Tobacco; Trichomes.

Gregory J. Anderson and Gabriel Bernardello

inflorescence group of flowers or arrangement of flowers in a flower head

pentamerous composed of five parts

campanulate bell-shaped

gynoecium the female reproductive organs as a whole

pistil the female reproductive organ

Soybean

Soybean, *Glycine max*, is an important crop throughout the world. Soybean is a source of food, oils—both culinary and industrial—and animal feed. In addition, soybean products can be found in plywood, particleboard, printing inks, soap, candy, cosmetics, and antibiotics.

Cultivated soybean and its wild ancestor, *Glycine soja*, are members of the legume family, Fabaceae. Legumes are particularly valuable because, in conjunction with symbiotic bacteria, they fix atmospheric nitrogen and they are excellent sources of protein, with soybeans containing the highest level of this nutrient.

The cultivated soybean plant is an erect, bushy annual. Plants produce clusters of three to fifteen purple or white flowers that develop into pubescent (fuzzy) pods, usually containing two to four seeds. Soybean seeds vary in size and are commonly yellow in color, but can also be green, black, or brown. Soybean varieties are classed into thirteen maturity groups according to their response to day length; the earliest group, 000, developed for far northern latitudes and the latest group, X, for tropical regions. Groups 000 through IX are grown across the central and eastern United States from Minnesota and North Dakota in the north to Florida and southern Texas in the south.

The soybean originated as a cultivated crop in northeast Asia about four thousand years ago. The earliest written record of the soybean plant is from China in 2838 B.C.E. Early farmers grew soy for their own food as well as for livestock feed. Soybean came to the United States in the late 1700s, but was used primarily as a forage crop until the beginning of the twentieth century.

Soybean is planted in the spring with row spacing averaging twelve inches using a grain drill. A skipped row system allows **cultivation** without damage from tractor tires. Nitrogen fixation by the symbiotic *Rhizobium* bacteria alleviates the need for nitrogen fertilizer, although soil testing may indicate other needed nutrients. Weed and insect pest controls are practiced

cultivation growth of crop plants, or turning the soil for this purpose

A soybean plant with pods in a field near Hutchinson, Kansas.

as needed. Soybean is harvested when the pods are dry and brown and the leaves have fallen, generally after the first freeze in the fall. The crop is harvested with combines that cut the plants and thresh the seed from the pods.

More soybeans are grown in the United States than in any other country in the world. Soybean is the second largest crop produced in the United States after corn. Over half of the soybeans produced in this country are exported to other parts of the world, making soybean an important part of the market economy of the United States.

Greater than half of the vegetable oil consumed in the United States is soy oil, a healthy vegetable oil high in unsaturated fats. Culinary soybean products include extracted soy protein, tofu (soybean curd), tempeh (fermented soybean mash), soy sauce, soy flour, edamame (green vegetable soybeans), soy sprouts, and soymilk. Other important soybean products are the animal feeds made from the meal that is one of the end products of oil extraction, and oil for light industrial purposes. SEE ALSO AGRICULTURE, MODERN; ECONOMIC IMPORTANCE OF PLANTS; FABACEAE; NITROGEN FIXATION.

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Speciation

Speciation can be defined, in a general way, as the various processes by which new species arise. Speciation mechanisms can be categorized in several ways. Some species arise by the divergence of two or more new species from a single common ancestral species (divergent speciation), while others arise from **hybridization** events involving two parental species (hybrid speciation). When a hybrid speciation event occurs, the newly derived species may have the same chromosome number as its parents (homoploid hybrid speciation), or it may have a higher number (polyploid hybrid speciation). In the latter case, the chromosome number of the newly derived species is usually the sum of those of its parents. In fact, polyploid hybrid speciation is one of the most frequent speciation mechanisms in plants.

hybridization formation of a new individual from parents of different species or varieties

Criteria for Recognizing Species

Because two major criteria for the recognition of species are in wide use in biology, any discussion of speciation processes should refer to the criteria under which species are recognized. Criterion 1 is known as the phylogenetic species concept. Criterion 2 is known as the biological species concept. Under either criterion (genetically distinct groups or reproductively isolated groups), species exist as one or more local **populations**. Most mating events involve individuals from just one population, and if local populations are small, all of the individuals within each one are closely related. However, there is often some degree of migration of individuals between populations by processes such as seed dispersal. Thus, the various local populations of a species may be loosely connected—by occasional interbreeding among them—into a larger population system, or reproductive community. Regardless of whether species are regarded as fully differentiated population systems (criterion 1), or population systems between which there is a genetically based barrier to reproduction (criterion 2), speciation processes involve the generation of two or more population systems from a common ancestor (divergent speciation) or the generation of a population system following one or more mating events involving individuals of different species (hybrid speciation). Because the two major species concepts recognize species on the basis of different criteria, a speciation event may be regarded as being complete when evaluated under criterion 1 while it is still in progress when evaluated under criterion 2.

population a group of organisms of a single species that exist in the same region and interbreed

Allopatric Speciation

Divergent speciation events can be categorized as those in which the populations that are separating into different species are geographically separated from each other (allopatric speciation) and those in which they are in close proximity (sympatric speciation). An allopatric speciation event begins with a single species that has allopatric (other land) populations, that is, populations that are geographically separated from each other and therefore in little or no contact with each other. This situation may arise when a long-distance dispersal event results in the founding of a new population that is distant from other populations of the species. An example of this would be an allopatric distribution of a species on two islands following the dispersal of one or more airborne seeds of a species from one island to the other. Allopatric distributions also arise when a widespread population system becomes fragmented into two or more allopatric systems by the formation of barriers to dispersal or by changes in climate. The rise of the Rocky Mountains and the corresponding formation of deserts and prairies in the North American interior have created unsuitable habitats for many plant species of temperate forest environments. These species, which at one time had continuous distribution ranges across the continent, became restricted to the forests of eastern and western North America. Once a species comes to have an allopatric distribution, the separate populations begin to evolve independently, and eventually they may become differentiated from each other. This differentiation may have an adaptive basis, as the populations evolve in response to different environmental conditions. Alternatively, the differentiation may be nonadaptive and simply reflect the random origins (by mutation) and genetic fixation of new characteristics that have little or no adaptive value. This is particularly likely to occur when one of the populations is very small, as is likely to be the case when a new population is founded by a long-distance dispersal event. Although the newly formed population may grow quickly, all individuals are descended from the small number of individuals that founded the new population (possibly just one individual). A population of this sort is described as having experienced a founder event, in which it goes through a "genetic bottleneck" and characteristics that were rare in the ancestral population but happened to occur among the founding individuals of the new population may occur in all individuals of the new population under these various circumstances.

As differentiation of allopatric populations proceeds, the point is eventually reached at which two species are recognized. Under the phylogenetic species criterion (criterion 1), speciation can be regarded as having been completed as soon as there are one or more genetically determined differences between the two populations, such that all individuals of one population are distinct from all individuals of the other. For example, all individuals on one island may have teeth on the margins of their leaves, while all of those on another island may lack such teeth. An intermediate stage in this process could be recognized when a particular characteristic is present in only one of the populations (possibly having arisen as a new mutation in that population), but this characteristic does not occur in all individuals of that population.

Reproductive Isolating Barriers

In the example just presented, the two populations still may not be recognized as separate species under the biological species criterion (criterion

Gloxinia sinningia hybrid, a product of speciation.

2) even after complete differentiation in one or more characteristics has occurred. Because criterion 2 involves the presence of a genetically determined reproductive isolating barrier (RIB), genetic differentiation in any number of characters, if maintained only by the geographic isolation of the populations, generally is regarded as an insufficient basis for the recognition of the two populations as separate species. Therefore, application of criterion 2 involves the assertion that genetically distinct and allopatric population systems may belong to the same species, and what is recognized as a speciation event under criterion 1 may be regarded as only the initial stages of a speciation event under criterion 2. However, if the two distinct populations later occur in sympatry—for example, following disperal of one of them into the range of the other—a test of sympatry occurs, and the presence or absence of RIBs can be evaluated. If these exist, criterion 2 is satisfied.

RIBs can be categorized in several ways. One useful distinction is between those that operate prior to fertilization (pre-fertilization RIBs) and those that operate afterward (post-fertilization RIBs). Fertilization is a critical point in the reproductive cycle of plants, because this is the point at which an ovule either begins to develop into a seed or is lost to the population. One example of a pre-fertilization RIB is the establishment of a different floral structure so that pollinating insects do not place the pollen from individuals of one plant species on the stigmas of individuals of another species, even if they visit plants of different species in succession. If a visit to the flower of one species results in the placement of pollen on the bee's back, but the stigma of another species is touched only by the underside of a visiting bee, cross-pollination and cross-fertilization will not occur. There are many cases of differing floral structure in the orchid family (Orchidaceae), in which natural pollinators do not cross-pollinate two closely related species, even when individuals of the two species grow side by side, but hybrids are easily generated when human investigators transfer the pollen from one species to the stigma of the other. In a natural setting, the two species are genetically isolated by a pre-fertilization RIB, and thus are recognized as separate species under criterion 2 as well as under criterion 1. Another form of pre-fertilization RIB is temporal isolation (isolation by time). In this case, two closely related plant species may flower at different times of the year or day and cross-pollination therefore does not occur. However, under controlled environments, with appropriate day-lengths and temperatures, plants of two different species may be induced to flower at the same and cross-pollination may occur.

Hybridization

interspecific hybridization hybridization between two species

viable able to live or to function

An example of a post-fertilization RIB is hybrid inviability. In this case, **interspecific hybridization** may occur under natural settings, but the offspring of such crosses may die soon after seed germination. Another example of a post-fertilization RIB is hybrid sterility. In this case, the hybrid individuals may be **viable** yet they fail to produce gametes, and therefore fail to reproduce. In this case, natural hybrids may be present and even abundant in natural settings, but the two parents of these hybrids are recognized as belonging to separate species under criteria 1 and 2. However, pollen and ovules are wasted by both species. This is a particular problem when two species occur in close proximity to each other and are isolated only by a post-fertilization RIB. In such cases, each of the two species is wasting some of its pollen and seeds and the reproductive potential of both species therefore is lessened. Furthermore, hybrid individuals, even if they are sterile, may compete with one or both of the parental species for habitat and pollinators. In such cases there will be selection against those individuals that cross with individuals of the other species, and any mutation that arises in one of the parental species and contributes to a pre-fertilization RIB is likely to become established in addition to the post-fertilization RIBs that already exist. In this manner, reproductive isolation can be reinforced between two species that are in geographic proximity yet are able to hybridize.

lineage ancestry; the line of evolutionary descent of an organism

Hybrid speciation events must, of course, involve species that occur in sympatry. Although it may seem contradictory to speak of hybridization between species when (at least under criterion 2) species are reproductively isolated population systems, it is often the case that reproductive isolation is strong but not absolute, and in such cases viable, fertile hybrids may occasionally arise between sympatric species. In homoploid hybrid speciation events, hybridization occurs between two species and thereby generates plants with a combination of characteristics that does not occur in either of the parental species. The hybrids may be better adapted than either parental species to a particular habitat, and a new and successful **lineage** therefore may be initiated and may spread into a habitat that is unoccupied by the parental species. Eventually, if RIBs develop, a new species can be recognized under both criteria 1 and 2. At least three cases of homoploid hybrid speciation have been documented in native sunflowers of North America.

Polyploid hybrid speciation is extremely common in many plant groups, notably in ferns, the grass family (Poaceae), and the sunflower family (Asteraceae or Compositae). Like homoploid hybrid speciation, a polyploid speciation event is initiated by a hybridization event. However, reproductive isolation between the new species and both of its parents is usually established immediately, in the form of hybrid sterility, a post-fertilization RIB. Polyploid species usually have two complete sets of chromosomes from each parent, and any hybrids that are formed between the new species and either of the parental forms are likely to experience irregular meiosis and thus to be sterile. SEE ALSO Evolution of Plants; Hybrids and Hybridization; Polyploidy; Species.

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Species

The term *species*, in the most general sense, refers to the various kinds of living things. Thus, species are generally recognized as distinct, fully differentiated groups of organisms. However, most modern definitions of species also recognize them as reproductive communities and acknowledge that mating occurs between members of each species but does not occur (or occurs only rarely) among members of different species. Species are therefore generally recognized as genetically differentiated, reproductive communities within which there is a pattern of ancestry and descent among organisms. Although most scientists accept this general definition, there are two somewhat different criteria that are often employed in the recognition of species, and the application of the two criteria does not always lead to the same conclusions.

The Role of Interbreeding

The first major criterion for the designation of species is the actual occurrence of interbreeding among the various organisms and **populations** within a species and the absence of such interbreeding between species. However, patterns of interbreeding are difficult to observe directly, particularly among plants that may live for hundreds of years. For this reason, indirect evidence regarding patterns of interbreeding is usually provided by the study of the patterns of differentiation among populations in genetically determined characteristics. In a trivial sense, oak trees and daisies are regarded as belonging to different species because they are distinguished by numerous characters and because hybrids between them are never observed. Thus, it is reasonable to conclude that they are not part of the same reproductive community. However, there are many recognized species of daisies, and many recognized species of oaks, and these species often are delimited by subtle differences. Consequently, one might examine several populations of daisies and observe that the plants are identical except for one character: the occurrence of a line of hairs along the undersides of the leaves. If all of the individuals in some populations have the line of hairs, and all of the individuals in other populations lack these hairs, there is evidence that two population systems exist and that there is no gene flow between them. In contrast, if each population that is examined includes individuals with the line of hairs and other individuals without the line of hairs, it can be concluded that this is simply a character that varies within a single species, like blood types in humans. Under this criterion, two species can be recognized even when the differences between them are not readily observable. For example, there are many documented cases in which two

population a group of organisms of a single species that exist in the same region and interbreed

or more population systems differ from each other by genetically determined differences that can only be detected by biochemical tests. Though they are difficult to distinguish, the species are recognized as distinct genetic communities.

Reproductive Isolating Barriers

The second major criterion of species status is the existence of a genetically determined barrier to gene flow between species. Such a barrier, known as a reproductive-isolating mechanism or a reproductive isolating barrier (RIB), prevents members of two different species from interbreeding, even if they occur in the same location. For example, the pollen that is produced by plants of one species may not germinate when placed on the stigmas of plants of another species and, thus, there can be no reproduction or gene flow between them. In this case, the RIB is the pollen/stigma incompatibility. Because this barrier is genetically determined, the two are regarded as reproductively isolated, and, as a result, two species are recognized.

Generally, any species boundary due to a reproductive isolating barrier also serves to prevent interbreeding as defined by the first criterion, but there are many instances in which the first criterion is satisfied while the second is not. The line of hairs on the underside of the leaves, which distinguishes two species of daisies under the first criterion in the example just described, does not by itself prevent interbreeding from occurring between the two kinds of daisies. The two daisy species may fail to exchange genes not because of a genetic mechanism but because they occur on different sides of a mountain range. Some biologists argue that if a RIB is not identified, the two kinds of daisies (one with the line of hairs, the other lacking it) should be grouped together and recognized as belonging to the same species. Others argue that the two populations are, indeed, persisting as separate and fully differentiated reproductive communities. Although they may have the potential to interbreed, the available evidence suggests that this does not occur, so they should be recognized as different species. Whatever position one takes on this matter, it should be noted that most species that have been recognized by science have, in fact, been delimited according the first criterion. SEE ALSO CULTIVAR; HYBRIDS AND HYBRIDIZATION; SPECIATION; TAXONOMY; VARIETY.

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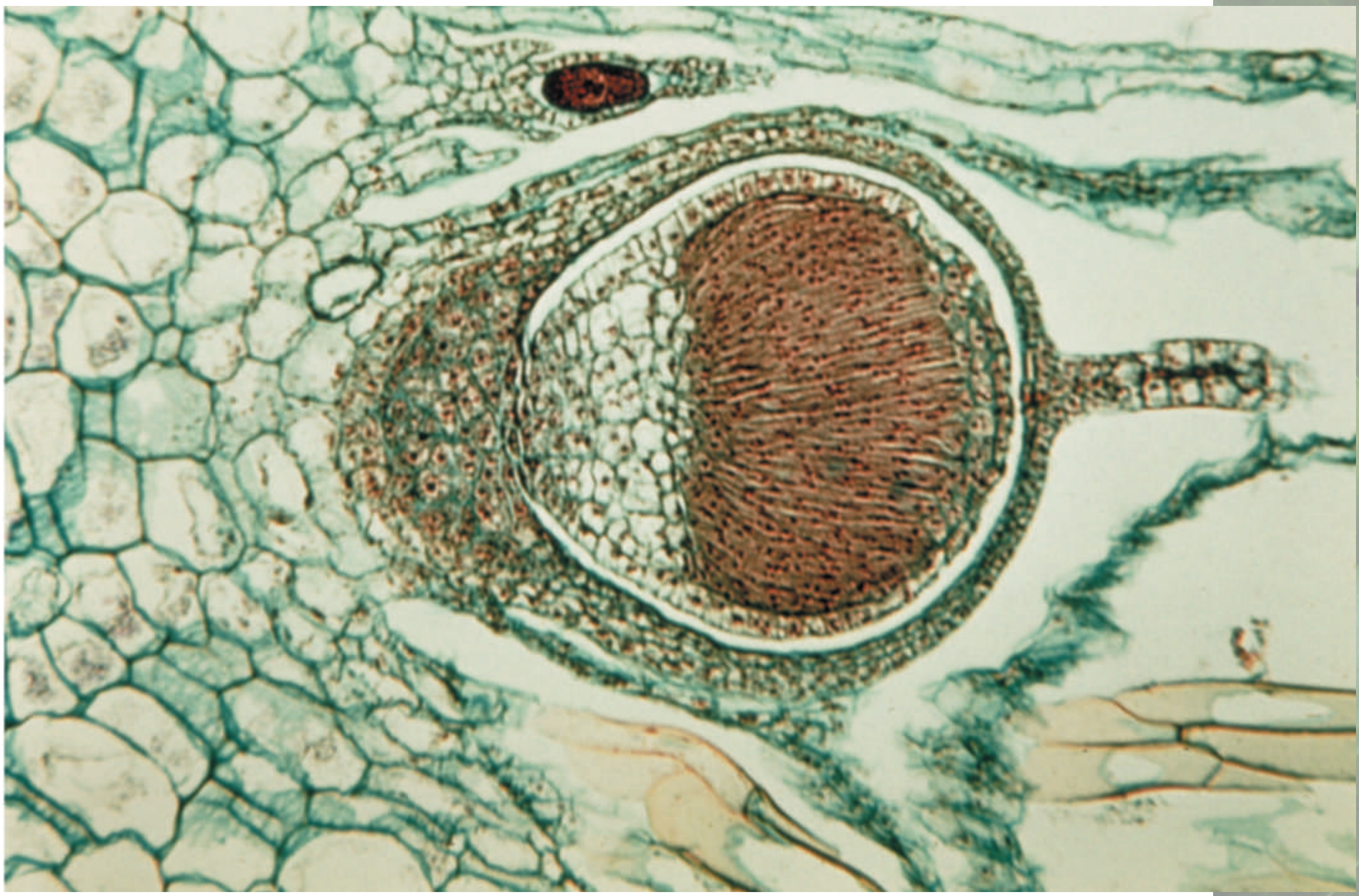
Spice *See Herbs and Spices.*

Sporophyte

diploid having two of each type of chromosome; twice the haploid number

Sporophyte, which literally means "spore-bearing" plant, is the **diploid** multicellular phase of an organism that displays alternation of generations. The sporophyte phase develops from the fertilized egg, or zygote, by sim-



Sporophyte of a *Marchantia* liverwort, composed of three parts (from left to right): foot, seta, and sporangium.

ple cell division and subsequent differentiation. Sporophytes occur in a few algae and aquatic fungi, and are universal in true plants. They differ greatly in size and level of complexity. In bryophytes the sporophyte is short-lived and permanently attached to the female parent, upon which it is nutritionally dependent. In all other plants, the sporophyte becomes independent of the female parent soon after embryological development is completed and remains as the dominant, photosynthetic stage of the plant. In the simplest case, a sporophyte can consist of only a capsule, or sporangium, as in the liverwort *Riccia*, but usually it will also possess one or more vegetative organs. For example, in mosses the sporophyte consists of a foot; a green, stemlike **seta**; and a single complex sporangium, while in pines it is a highly branched tree with roots, stems, leaves and thousands of sporangia. Within the sporangia, which are the reproductive organs of the sporophyte, **haploid** spores are produced by **meiosis**. Germination of these spores marks the beginning of the haploid, sexual phase of the life cycle. SEE ALSO Bryophytes; Gametophyte; Reproduction, Alternation of Generations and; Reproduction, Asexual; Reproduction; Sexual.

Barbara Crandall-Stotler

seta a stiff hair or bristle

haploid having one set of chromosomes, versus having two (diploid)

meiosis division of chromosomes in which the resulting cells have half the original number of chromosomes

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Stems

The body of a land plant is composed of a shoot system and a root system. The shoot includes the stem, leaves, and other reproductive systems. The stem is the axis or supporting column of the shoot system, providing support for the leaves and the reproductive structures. It is the channel through which water and mineral elements derived from the soil flow from the roots to the upper parts of the plant. It is also the route taken by organic products synthesized in the leaves when they are transported to other plant parts.

Anatomy

The structure of the stem is organized around the vascular or conducting system, which in seed plants consists of an interconnected pattern of bundles extending lengthwise in the stem. At each node, or site of leaf attachment, one or more of the bundles bends outward into the petiole (leaf stalk) to provide the vascular supply of the leaf, the leaf trace. Despite this constant loss of bundles into the leaves, the number remains constant because of branching within the stem. Each bundle consists of two tissues, the inner xylem, which is the channel for water and dissolved minerals, and the outer phloem, which transports the organic products of photosynthesis.

parenchyma one of three plant cell types

stomata openings between guard cells on the underside of leaves that allow gas exchange

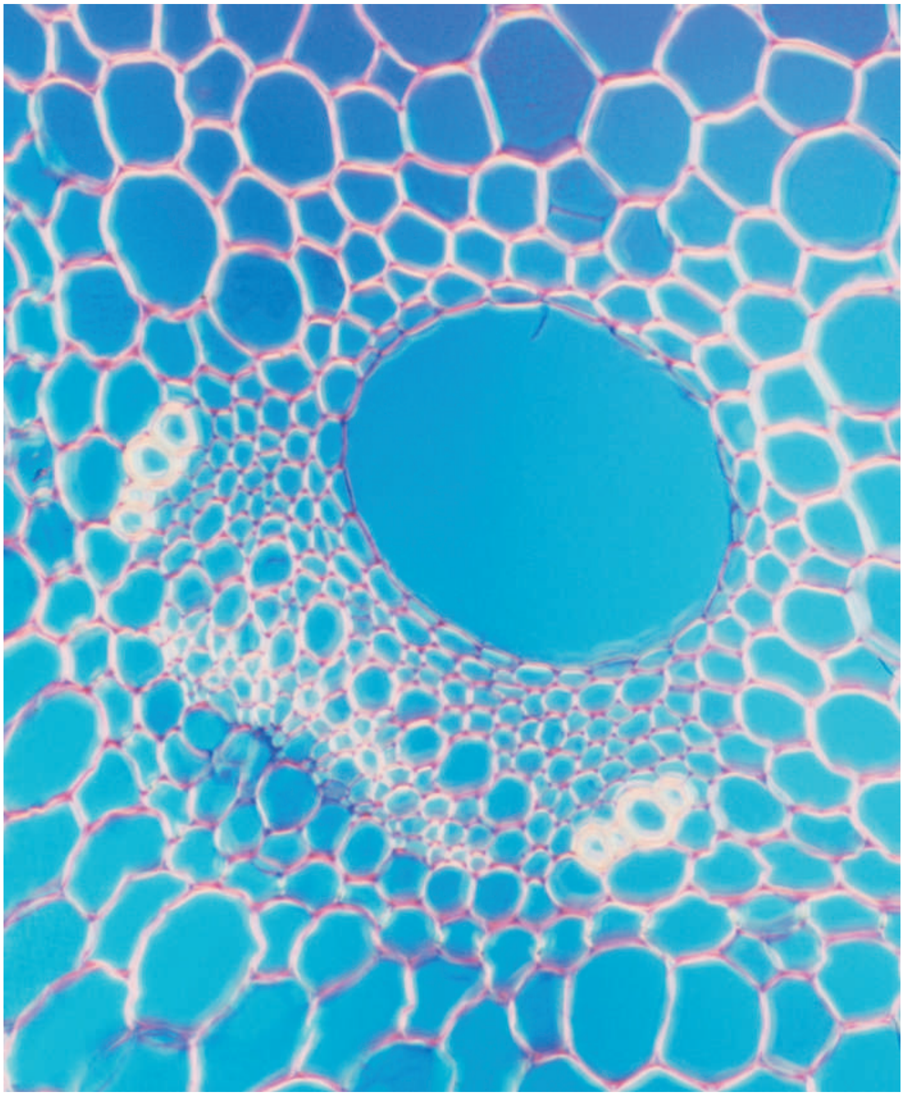
In dicotyledorous plants the bundles are arranged in a ring around a central pith composed of thin-walled **parenchyma**. The bundles themselves are surrounded by the cortex, which consists of parenchyma often with additional supporting tissues. The entire structure is bounded by the epidermis, which prevents excessive water loss. In many herbaceous plants the cells of the cortex contain chloroplasts and are photosynthetic, and the surrounding epidermis includes the **stomata** necessary for gas exchange. In the monocotyledons, such as lilies and grasses, the vascular bundles are not arranged in a ring but are distributed through the central region of the stem inside the cortex.

Growth

apical meristem region of dividing cells at the tips of growing plants

primordia the earliest and most primitive form of the developing leaf

Unlike animals, which ordinarily reach a final stable size, plants continue to grow throughout their lives. This indeterminate growth is accomplished by means of meristems. Growth of the stem, and of the entire shoot, is accomplished through the activity of the shoot **apical meristem** located at the tip of the stem. This region of continued cell division gives rise to the tissues of the stem and also to the **primordia** of the leaves that the stem bears. The leaves are initiated in a regular pattern and develop to mature size along with the tissues of the stem. Although the tissues of the stem are initiated by the apical meristem, much of the growth takes place below the meristem as the tissues are acquiring their mature size and functional properties through the process of differentiation. When initiated by the apical meristem, the leaf primordia are very close together; the growth that occurs below the meristem is by expansion of the internodes (regions between the leaf attachment points). Elongation of the internodes separates the leaves to their final positions. In some plants the expansion of the internodes is limited so that the mature leaves are close together and the stem is very short. This is seen, for example, in rosette plants such as the dandelion.



A bundle of vascular tissue in the stem of a horsetail plant (*Equisteum max*) magnified two hundred times. In stems, monocots have scattered vascular bundles while dicots and gymnosperms have vascular bundles in a ring.

One further aspect of growth is very important for trees or shrubs; this is the formation of a woody secondary body. A meristem known as the vascular cambium develops between the xylem and the phloem in the bundles. Divisions of this cambium form a layer of xylem to the inside and of phloem to the outside. This secondary production of tissue may be limited if the life of the stem is short, but in long-lived trees it may build up a trunk of extensive dimensions. The development of the secondary body expands the stem **laterally.** If continued for any length of time, this lateral growth ruptures the protective epidermis. Continued protection is provided by the formation of the cork cambium, which lays down a layer of largely impervious cork tissue.

laterally away from the center

Branching

In many of the lower vascular plants the stem branches by the subdivision of the apical meristem into two portions each of which forms a branch stem. In the seed plants, however, branches are formed through the development of buds formed in leaf **axils**, that is, on the stem just above the point of attachment to the leaf. Typically a small portion of the apical meristem is detached, or left behind, in the axillary position as the apical meristem

axils the angle or crotch where a leaf stalk meets the stem advances and this forms a daughter apical meristem that initiates leaf primordia and forms an **axillary bud**. These often become arrested after a certain degree of development is attained, remaining suppressed by the apical meristem. When released, such a bud expands to form a branch, a replica of the main axis. In addition to this regular pattern of branching, many plants form buds capable of developing into new shoots in various locations other than leaf axils, including roots. Such buds are called **adventitious**.

axillary bud the bud that forms in the angle between the stem and leaf

adventitious arising from secondary buds

Modified Stems

There are many ways in which the basic form of the stem deviates from the typical pattern just described, and some of these are of economic significance. In the strawberry, for example, branches called runners extend over the ground, take root at nodes and establish new plants. This natural means of reproduction is used to **propagate** the plant commercially. The same kind of structure but extending underground is called a stolon; when it is the main axis of the plant it becomes a rhizome. Rhizomes may become enlarged and serve as repositories for stored nutrients that may be economically important.

propagate to create more of through sexual or asexual reproduction

Another similar structure develops when the terminal portion of a stolon enlarges to form a tuber, as in the potato. A corm, seen in the gladiolus, is an upright underground stem that is greatly swollen with stored nutrients. The superficially similar bulb, as in the onion, has a much reduced stem and the stored materials are in fleshy leaf bases. In some cases stems may become broad and flattened to resemble leaves, and are called cladophylls. Many plants of desert or salty environments become very **succulent** or fleshy and bear reduced leaves. Stems may also assume a protective function by developing sharp, hardened tips as spines, while others form tendrils, which may help climbing stems to attach to their support. SEE ALSO Anatomy of Plants; Germination and Growth; Meristems; Phyllotaxis; Potato; Shape and Form of Plants.

succulent marked by fleshy, water-holding leaves or stems

Taylor A. Steeves

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Succulents

The term *succulent*, when applied to plants, refers to those organisms that have very fleshy leaves or stems, regardless of whether they are adapted to dry habitats (as are most true succulents). Specifically, succulent plants are those that are strongly adapted to life in water and/or heat-stressed habitats, and are typically represented by members of certain plant families (see accompanying table). Plants that have evolved in very hot, dry conditions, or those that experience these conditions at certain times of the year, have evolved various structures, habits, and metabolic mechanisms to cope with existence in stressed habitats.

FLOWERING PLANT FAMILIES CONTAINING SUCCULENTS

Family	Common Name	Geographic Distribution*	Number of Species (approximate)	Examples of Succulent Genera
Agavaceae	Agave family	North America, Africa	625	*Agave, Dasylirion, Nolina, Sanseiveria, Yucca*
Aloaceae	Aloe family	Africa	440	*Aloe, Gasteria, Haworthia*
Aizoaceae	Ice plant family	Africa	1,300	*Carpobrotus, Faucaria, Lithops, Pleiospilos*
Asclepiadaceae	Milkweed family	Africa	>2,000†	*Ceropegia, Huernia, Orbea, Piaranthus, Stapelia*
Cactaceae	Cactus family	North and South America	1,600	*Carnegiea, Ferocactus, Mammillaria, Opuntia*
Crassulaceae	Stonecrop family	Africa, Asia, Europe	1,500	*Crassula, Echevaria, Kalanchoe, Sedum*
Didiereaceae	Didieriea family	Madagascar, Africa	11	*Allauadia, Decaryia, Didierea*
Euphorbiaceae	Euphorbia family	Africa, North America	5,000‡	*Euphorbia, Jatropha, Monadenium*
Portulacaceae	Purslane family	Africa, Australia, North and South America	250	*Anacampseros, Ceraria, Portulaca*

* For succulent members of the family.
† Approximately 450 species are succulent.
‡ Approximately 750 species are succulent.

Most succulents are xerophytes, that is, plants that have developed adaptive features for life in dry, often hot, environments. In addition to some shared features with nonsucculent xerophytes, succulent plants have acquired additional specialized features, independently, in several different plant families. The general characteristic of plants that have evolved succulence is the presence of large **parenchyma** cells in leaves or stems (and occasionally in roots) that serve the purpose of water storage. Furthermore, these plants may also possess one or more of the following adaptations to reduce water loss during periods of heat or drought stress: the presence of epidermal cells with thickened outer walls; increased accumulation of the waxy **cuticle** layer covering the epidermis; and the evolution of **crassulacean acid metabolism** (abbreviated CAM; this process delays gaseous exchange through **stomata** until nighttime, when temperatures are lower and water lost by **transpiration** is decreased). SEE ALSO CACTI; DESERTS; DEFENSES, PHYSICAL; PHOTOSYNTHESIS, CARBON FIXATION AND.

Robert S. Wallace

parenchyma one of three types of plant cell

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

crassulacean acid metabolism water-conserving strategy used by several types of plants

stomata openings between guard cells on the underside of leaves that allow gas exchange

transpiration movement of water from soil to atmosphere through a plant

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Sugar

Sugar, from the Greek word *saccharis*, is a term with a variety of meanings. To the biochemist, sugar is a broad term covering a large group of related organic **compounds**, all of which are composed of carbon, hydrogen, and oxygen. Green plants utilize their chlorophyll to transform solar energy (sunlight) into chemical energy by converting carbon dioxide and water into plant sugars through the process of photosynthesis. Generally, when people speak of sugar, they are referring to sucrose, which is a disaccharide or double sugar composed of equal parts of glucose and fructose. Glucose and fructose are monosaccarides or single sugars, found in fruits and in honey (together with sucrose). There are hun-

compound a substance formed from two or more elements

dreds of different sugars and these are only a small section of the vast family of carbohydrates, which includes cellulose at one end of the scale and simple alcohols at the other. Starches, also made by plants, are dense complexes of sugar molecules. Starches and sugars make up the group of foodstuffs known as carbohydrates. All carbohydrates are formed originally by photosynthesis.

Sources of Natural Sugar

Sucrose, fructose, dextrose, and glucose are the natural sugars most frequently used. Although many fruit-bearing plants like the date palm and the carob produce sugar as a product of photosynthesis, the world's major supply of sugar is obtained from the cultivated or managed crops of sugarcane, sugar beet, corn, sugar maple, and sweet sorghum. Sugarcane, corn, and sweet sorghum are cultivated grass plants that store sugar in their stalks or seed. Sugar beet is a broadleaf plant that stores sugar in its root. Sugar maple is a hardwood tree with sugar in its sap, and honey is produced by honey bees from the nectar of plant flowers that contains sugars.

Sugar, Calories, and Energy

In addition to its flavor, which was the original reason for its popularity, sugar supplies an important nutritional factor in the form of energy. Sugar contains four calories per gram and one teaspoon of white table sugar (sucrose) weighs about 3.5 grams. The basic calorie requirement for maintaining life (respiration, circulation, muscle tone) varies between 750 and 1,630 per day in a state of complete rest. Intense muscular effort may require upwards of 7,000 calories during the day. Carbohydrates are an essential component of the human diet, and Recommended Dietary Allowances (RDAs) for nutrients in the American diet have been established by the National Academy of Sciences. The RDAs suggest that the average dietary energy intake (in calories) should consist of 10 to 15 percent protein, 35 to 40 percent fat, and 45 to 50 percent carbohydrates. Carbohydrates, therefore, contribute the major part of the available energy in the human diet. In less-developed areas, it is not unusual to find 80 to 90 percent of available energy in the diet coming from carbohydrate sources.

To get the energy needed, humans reverse the process that plants utilize to make sugar. Digestion of sugars (carbohydrates) is accomplished by **enzymes** beginning in the mouth and continuing in the small intestine. In the cells of the human body, all usable carbohydrates are converted to the same basic fuel, **pyruvic acid**, which is then burned to release energy, stored as fat for future energy needs or converted to intermediates for growth or maintenance of body tissue. Although proteins and fats can also be used as sources of energy, only sugars can yield pyruvic acid. That is why sugar is the principal and preferred fuel for the body's energy cycle.

enzyme a protein that controls a reaction in a cell

pyruvic acid a three-carbon compound that forms an important intermediate in many cellular processes

Social and Environmental Impact

During its long history, sugar has been the cause and prize of wars, as well as the object of political activity. There are logical reasons for this. Sugar is an attractive commodity and thousands of people throughout the world gain their livelihood from sugar. With a rapidly expanding world

Sugar beets on a Nebraska farm about to be processed for their sugar.

population, this is important because sugarcane and sugar beet are, respectively, the most efficient plant fixers of solar energy among tropical and temperate-zone vegetation. Sugarcane is four times as effective as any tropical plant in terms of dry-matter production per unit of land, and sugar beet is twice as productive as any temperate-zone plant. It requires an average of only 0.07 hectare (0.17 acre) to fix solar energy to the equivalent of one million kilocalories of energy in the form of sugar. All other forms of edible energy require more. Beef is at the top end of the scale, needing 7.7 hectares (19 acres)—more than one hundred times as much land as needed for sugar.

Processing and Marketing

Crystallized sugar, which is the basic commodity of the international sugar trade, comes from sugarcane, grown in warm, moist climates, and sugar beet, grown in temperate climates. Juice containing sugar is extracted from the stalks of sugarcane and from the roots of sugar beet. The process of crystallization separates sugar out of a sugar-saturated solution. It begins by the formation of minute crystals that act as nuclei for the growth of larger ones. The size of the crystals is controlled by temperature. The uniform small crystals in table or white sugar are the result of controlled crystallization.

Sugar in the international market is under the review of members of the International Sugar Agreement. About 70 percent of the world's sugar supply is consumed in the areas in which it is grown. Twenty percent is marketed through agreements or some form of preference. The remaining 10 percent is world market or free market, and is sold at a price that has no relationship to the cost of production.

Total caloric sweetener consumption in the United States is about 130 pounds per capita each year. Use of refined sugars (from sugarcane and sugar beet) has declined from 67 percent of total caloric sweeteners (84 pounds) in 1980 to less than 49 percent (63 pounds) in 1999. The principal reason for this decline is the increased per capita consumption of corn sweeteners, especially high fructose corn syrup. The approval of the artificial sweetener aspartame (for example, Nutrasweet) for table and industrial use in 1982 is another reason for this decline. SEE ALSO Carbohydrates; Economic Importance of Plants; Grasses.

Garry A. Smith

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Symbiosis

Symbiosis is simply defined as living together. Scientists use this term to describe intimate relationships between members of different species. By definition there are at least two species in a symbiotic relationship; it is unknown the maximum number of species that a symbiosis can sustain. This number may be very great; fungal partners (mycorrhizae) of plant roots link many photosynthetic plants of different species in one continuous networked symbiosis. Partners may belong to the same kingdom (for example, plants in symbiosis with other plant species) or may include partners from different kingdoms. A lichen symbiosis consists of partners from two or three kingdoms—a fungus, a **protist** (algae), and often a cyanobacterium (eubacteria). The smaller partner(s) are usually called the symbiont(s) and the larger partner the host. The host's cells, body, body surface, or even its home may be shared with its symbionts.

protist usually a single-celled organism with a cell nucleus, of the kingdom Protista

To what extent must two species live together be considered a symbiosis? A general rule is that the partners must spend a significant amount of time together (part or all of their life cycles). This sustained contact enables a relationship to develop that affects how both species adapt and evolve. The symbiotic relationship is usually classified as belonging to one of three types: mutualism (benefiting both partners), parasitism (one partner, the parasite, benefits at the expense of the host), or commensalism (one partner benefits while the other is unaffected). However, it is too simplistic to place symbioses into such restrictive categories since the environment and ecological interactions with other species may affect the nature of the relationship. Under one set of conditions a relationship may be characterized as mutualistic, while under different conditions it may be parasitic. For example, the relative benefit for plants to host ants as a way to defend them against **herbivores** depends on the degree of herbivory and must be weighed against the cost of synthesizing the nutritional **compounds** needed to support resident ants. Both of these are subject to external influences.

herbivore an organism that feeds on plant parts

compound a substance formed from two or more elements

Symbiosis provides an important source of evolutionary novelty. Special symbiont capabilities include photosynthesis and the transfer of photosynthetic products from **cyanobacteria** and algae to animal and fungal hosts, and the supply of nutrients (nitrogen fixation by bacteria in **legumes** and

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

legumes beans and other members of the Fabaceae family

SYMBIOTIC ASSOCIATIONS INVOLVING PLANTS OR PHOTOSYNTHETIC ALGAE PARTNERS

Type of Symbiotic Relationship		Partners	Nature of Interaction
Symbionts Living in Host	Lichen	**Symbionts:** Algae, cyanobacteria	Algae provide photosynthetic sugars and cyanobacteria provide nutrients (nitrogen)
		Host: Fungus	Fungus provides protection against environmental extremes
	Coral (and anemones)	**Symbionts:** Algae	Algae provide photosynthetic sugars
		Host: Cnidarian (animal)	Animal host provides recycled nutrients (nitrogen and phosphorus) and protection
	Bacteria–plant	**Symbionts:** Nitrogen-fixing bacteria (*Rhizobium,* actinomycetes, cyanobacteria)	Bacteria provide nutrients (nitrogen)
		Host: Plant (legumes, alders, cycads, *Azolla* ferns)	Plant host provides photosynthetic sugars
Symbionts Living on or in Intimate Contact With Host	Ant–plant mutualisms	**Symbionts:** Ant colonies	Ants provide defense against herbivores, nutrients from colony wastes, protection
		Host: Plant (e.g., acacia trees)	Plant host provides nutrition (nectar, food bodies) and shelter (hollow thorns)
	Plant–plant	**Symbionts:** Parasitic plant (mistletoes, *Rafflesia*)	Gains photosynthetic sugars, water, and other nutrition from host
		Host: Plant	Harmed only
	Mycorrhizae	**Symbionts:** Fungus (ectomycorrhizae include many basidiomycete fungi; endomycorrhizae include many ascomycete fungi)	Absorption of nutrients and water from soil; transfer of photosynthetic sugars among different plant species
		Host: Plant (many partners)	Plant host provides photosynthetic sugars

by cyanobacteria in cycads) to plant hosts. Other novel capabilities in marine animal symbioses include light production (luminous bacteria in marine fishes and invertebrates) and chemosynthesis by sulfur-reducing bacteria in hydrothermal vent host animals. In exchange for these services, the host provides the symbiont shelter and/or nutrition. These exchanges allow symbiotic relationships to thrive in marginal environments where resources such as energy and nutrients are limiting. Lichens are able to **colonize** bare rocks because the fungus provides shelter and protection against **desiccation**, its algal partners provide nutritional energy through photosynthesis, and its cyanobacteria provide nitrogen to the algae and to the fungal host. In the coral reef **ecosystem**, symbiotic algae called zooxanthellae photosynthesize and provide energy-rich sugars to their host corals. In nutrient-poor and sunlit tropical seawater, this symbiosis forms the base of the food web and supports the high diversity of all coral reef organisms. Other examples of mutualistic symbioses include the relationship between fungi and the roots of higher plants. Mycorrhizae (the fungal symbionts) associate with roots of higher plants and increase the water and nutrient uptake capabilities of plants. In return, they receive photosynthetic products from their host plants. In 1997, Suzanne Simard and her colleagues found that mycorrhizae connect and transport photosynthetic products between plants and trees in different environments. Other symbionts such as parasitic orchids take advantage of this association by connecting to the fungal network and withdrawing nutrients for their own use.

colonize to inhabit a new area

desiccation drying out

ecosystem an ecological community together with its environment

In parasitic symbioses, the parasite must avoid host defenses and obtain nutrients while remaining in or on the host. In so doing, the parasite often loses the ability to live independently. Plants such as dwarf mistletoes and the largest flower in the world, *Rafflesia*, have lost the ability to photosynthesize; they must derive nourishment from their photosynthetic host plants. These are considered to be obligate symbioses (one or more partners is de-

A *Rafflesia* flower at Poring Hot Springs in Sabah, eastern Malaysia. *Rafflesia,* which lost the ability to photosynthesize, must derive nourishment from their photosynthetic host plants.

pendent on another and cannot survive alone). Often these relationships include more than one partner, each with a different role in the symbiosis. For example, insect aphids specialized to suck plant juices from their hosts must rely on **intracellular bacteria** for essential amino acids not available in plant tissues.

intracellular bacteria bacteria that live inside other cells

The few examples of commensalistic symbioses are behavioral; one partner taking advantage of the activities of another to obtain food. It is unlikely that the unaffected partner is truly unaffected. If it is really unaffected, commensalism is difficult to define in the context of symbiosis. The definition of symbiosis usually assumes that an interaction is taking place, which means both partners must participate.

Flexibility in the type and amount of nutritional exchanges and in the roles of partners enables the symbiotic relationship to adapt and evolve over time to meet the different needs of the partners. A symbiont, host, or both may lose the ability to live independently because the partner has irrevocably assumed certain critical life functions. This concept is fundamental to the endosymbiotic theory of the origin of **eukaryotic** cells. Chloroplasts and **mitochondria** are the remnants of former symbionts that provided novel metabolic functions (photosynthesis and respiration) to their host cells.

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

mitochondria cell organelles that produce ATP to power cell reactions

Finally, symbiosis plays an important and often overlooked role in ecology. Nitrogen-fixing bacteria and mycorrhizal fungi provide nutrients to primary producers, and symbiotic associations like lichens are usually the first colonizers. Feeding interactions among symbiotic partners may increase the energy efficiency of food chains and promote nutrient recycling. When one thinks about saving species and **biodiversity**, the emphasis should be placed on understanding and preserving symbiotic relationships. If one partner is lost, all dependent partners will perish. It is rare that any species lives in isolation. SEE ALSO Coevolution; Endosymbiosis; Interactions, Plant-Fungal; Interactions, Plant-Insect; Interactions, Plant-Plant; Interactions, Plant-Vertebrate; Lichen; Mycorrhizae; Parasitic Plants.

Gisèle Muller-Parker

biodiversity degree of variety of life

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Systematics, Molecular

Molecular systematics is the use of molecules to determine classification systems and relationships. For hundreds of years botanists used **morphology**, or overall appearance, to identify and classify plants. Morphological systematics has been important for the basic understanding of plant evolution and relationships; however, it has limitations. One limitation to morphology in plants is homology. Homology assumes that two similar structures have the same evolutionary origin. In other words, the trait arose in an ancestor and was passed down to its descendants. Homology in plant morphology is frequently very difficult to resolve since plant structures can become modified into other forms (e.g., spines of cacti are modified leaves).

morphology shape and form

Just as a botanist may compare the shape of a leaf between two different plants, molecular **systematists** compare molecules. Molecules have an advantage over morphology in two aspects. First, homology is usually much easier to determine in molecules than in morphology. Second, molecules tend to provide many more pieces of information than can be gained from morphology. A scientist studying morphology may compare one hundred traits, but a scientist using molecules will compare several hundred to several thousand traits depending on the technique.

systematists scientists who study systematics, the classification of species to reflect evolutionary relationships

Early molecular systematics began with micromolecules. The earliest of these studies can be traced as far back as the 1880s, but much of the work was conducted between the 1950s and 1970s. Micromolecules are small molecules mostly responsible for colors, scents, and chemical defenses of plants. Chemicals found in different plants are identified and compared across species for similarities. Species sharing **compounds** are presumed to be more closely related. Later botanists used macromolecules, which are proteins and nucleic acids. Much of the work on proteins was conducted in the 1970s and consisted of determining the order of amino acids in specific proteins (protein sequencing) or determining whether different **populations** or species of plants had different forms of specific **enzymes** (isozyme variability). Other protein-based studies utilized principles of **serology** and created antibodies for protein extracts that were compared to extracts from a different species. The degree to which the **antibodies** of one plant matched the proteins of a another plant provides an estimate of how closely the two plants are related.

compound a substance formed from two or more elements

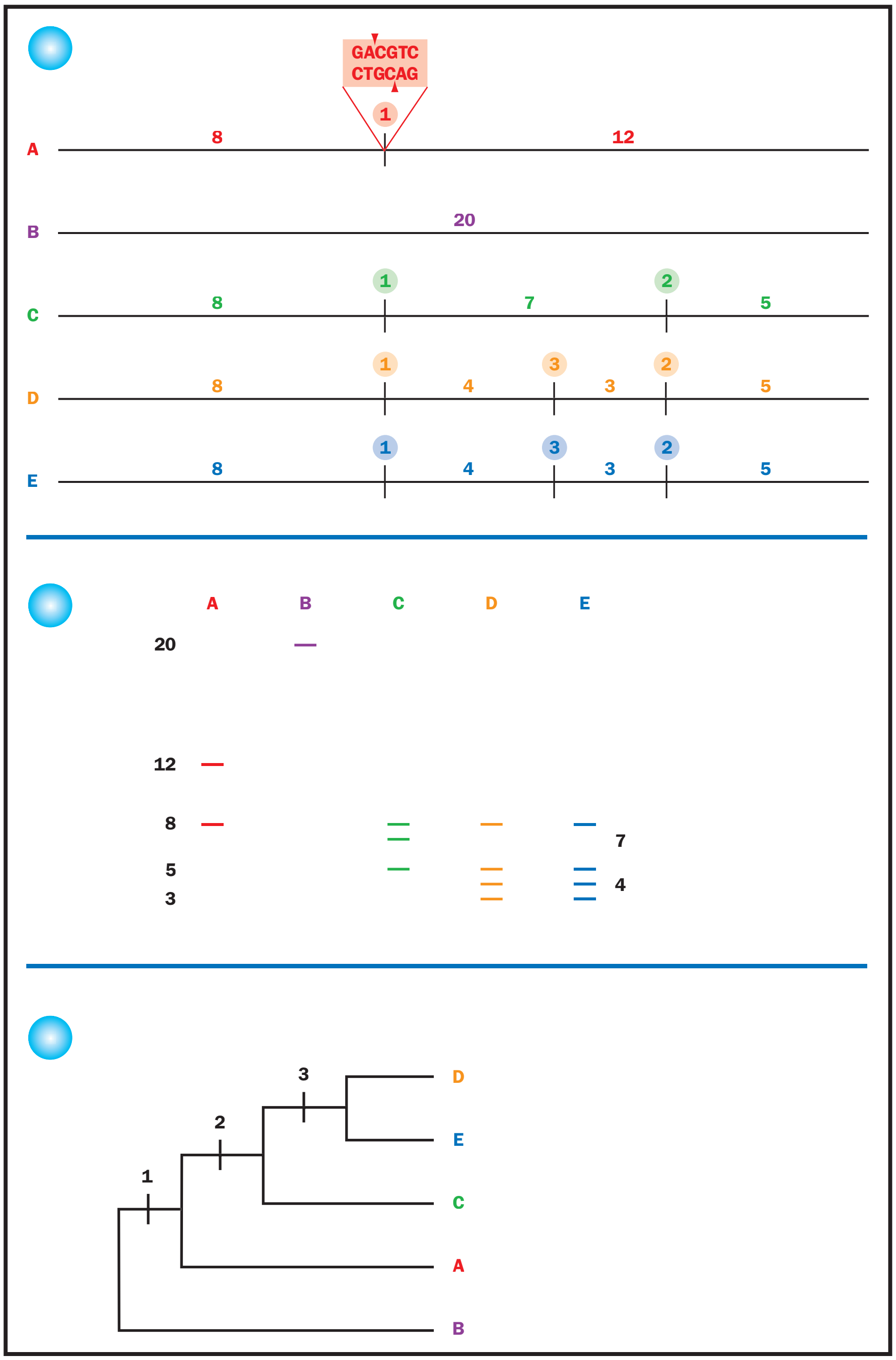
population a group of organisms of a single species that exist in the same region and interbreed

enzyme a protein that controls a reaction in a cell

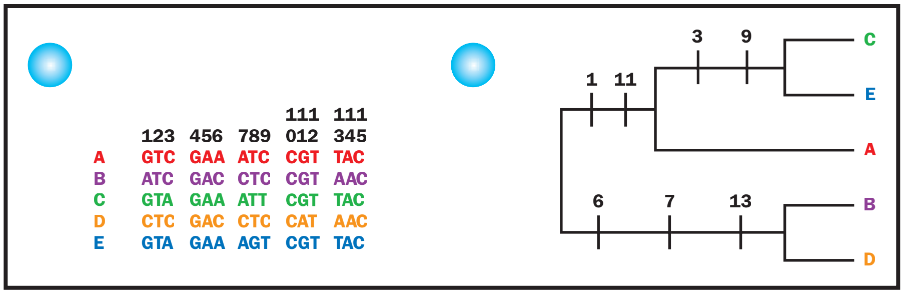
serology the study of serum, the liquid, noncellular portion of blood

antibodies proteins produced to fight infection

Studies began to use deoxyribonucleic acid (DNA) in the late 1960s and 1970s with DNA-DNA hybridization. This method uses the principle that DNA is a double-stranded molecule and that high temperatures (greater than 80°C) can cause all of the DNA to become single-stranded. When cooled, the DNA resumes its double-stranded nature (re-annealling) and the temperature at which it becomes completely double-stranded is an indication of how similar the strands of DNA are. In this method, DNA from two plants is combined and heated. If all of the DNA is from closely related plants, the re-annealling temperature is high. If the DNA is from two distantly related plants it is lower. The re-annealling temperature is an estimate of how similar the plants are. The closer the temperatures are to the re-annealling temperature of a single plant, the more closely the plants are assumed to be related.



A. Restriction site map for five plants labeled A to E. The numbers above the bars represent the distance between restriction sites (in units of one thousand nucleotides), which are the numbers in the circles. For plant A, the nucleotide sequence that is recognized by this restriction enzyme is enlarged and the areas where the enzyme cuts the DNA are shown with black carats. **B.** A drawing of what a gel would look like after restriction enzymes had cut the DNA for the five plants in A. Each bar represents a fragment and the fragment sizes are shown on the sides. **C.** A phylogeny for the five plants based on the restriction site variation shown. The sites are marked on the tree, where they are present for all plants farther up the tree.



A. A portion of an aligned sequence showing fifteen consecutive nucleotides for five plants labeled A to E. **B.** The phylogenetic tree generated from the data in A. Bars along the branches indicate where changes in the DNA sequence serve to unite two or more plants together. For example, since only plants B and D have the nucleotide C at position 6, this serves to put theses two plants in the same group.

During the 1980s botanists made comparisons of DNA between plants using restriction site analysis. Scientists used restriction enzymes that cut DNA into fragments of various lengths. These enzymes cut the DNA at specific combinations of nucleotides every time this combination of sequences is encountered. The fragments are separated by size using **gel electrophoresis** and visualized by a probe that matches specific regions of the DNA. Comparing fragment sizes, it is possible to determine whether a specific restriction site is present or absent in any given species. The presence of a restriction site in two or more plants implies that the plants with the site have a more recent common ancestor. Restriction site data are capable of producing hundreds of sites depending on the numbers of enzymes that are used. Most botanists use the DNA from the **chloroplast** since it is smaller in comparison to other regions of the **genome** and a number of probes are available.

gel electrophoresis a technique for separating molecules based on size and electrical charge

chloroplast the photosynthetic organelle of plants and algae

genome the genetic material of an organism

During the late 1980s and the 1990s molecular systematists made a shift to comparing DNA sequences. A specific gene or DNA region is selected and the order of nucleotides of that gene are determined (sequencing). DNA sequencing was made easier by the polymerase chain reaction (PCR), which allows millions of copies of a gene to be made (amplification) from a single copy. Once a gene is amplified, it is relatively easy to sequence. Nucleotide sequences generated from the same gene of different plants can be compared, or aligned. The traits that are compared are the nucleotides that occur at each aligned position in the gene. As with restriction sites, the shared presence of a specific nucleotide at a specific site in two or more plants is assumed to mean that these plants share a more recent common ancestor.

Many botanists utilize a gene called ribulose bis-phosphate carboxylast-oxygenase, large subunit, abbreviated rubisco, found in the chloroplast DNA. This gene is functionally important for plants as it encodes the enzyme that allows plants to make CO_2 into complex molecules. Because it is so important, changes in the gene sequence are infrequent, allowing botanists to use these changes to answer questions about relationships and origins of flowering plants. Recently, botanists have expanded the number of genes studied. Many genes are now used depending on the taxonomic level of interest. Genes with lesser, or no, function evolve quickly and are useful to compare species or populations. Genes with functional constraints are more useful to compare **genera** or families.

genera plural of genus; a taxonomic level above species

It is common for scientists to use several genes for a study. As more genes are added, it strengthens the results by adding more data, and from genes that may evolve differently. One important example of this is the comparison of nuclear genes to chloroplast genes. Chloroplasts usually are inherited through a single parent (the mother), whereas nuclear genes are inherited from both parents. If a botanist studies only chloroplast genes, it is possible that only the maternal **lineage** will be resolved. This is especially critical in plant groups that are known to hybridize. To counter this potential error, many botanists look at chloroplast genes in conjunction with nuclear genes. Common nuclear genes that are used are the ribosomal ribonucleic acid (RNA) genes. SEE ALSO PHYLOGENY; PLANT IDENTIFICATION; SYSTEMATICS, PLANT; TAXONOMY.

lineage ancestry; the line of evolutionary descent of an organism

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Systematics, Plant

Plant systematics is a broad discipline that is often defined as the study of the kinds of organisms (both living and fossils), and of the relationships among these organisms. Thus, students and researchers in the area of systematics (termed systematists) study the diversity of all life, including bacteria, fungi, plants, and animals, with several major goals. Systematics includes the identification, naming, and classification of plants, as well as the investigation of evolutionary relationships (phylogeny) and of evolutionary processes. As such, some consider systematics the fundamental discipline upon which all other areas of biology must rely. That is, other areas of investigation all depend on a clear understanding of species names, species delimitation, and organismal relationships. Thus, systematics is a unifying discipline and operates in a highly similar fashion regardless of the major group of organisms investigated (e.g., plants, fungi, animals, or bacteria).

Research in systematics may involve the collection of organisms in the field and the study of these organisms in their natural setting, in museums, and in the laboratory; the latter may employ approaches also used in molecular biology. The sources of evidence used in systematics are also highly varied and may include morphology, chemistry (a subdiscipline often referred to as chemosystematics), **paleobotany**, **physiology**, ecology, **biogeography**, and various sources of deoxyribonucleic acid (DNA)/ribonucleic acid (RNA) data (an area referred to as **molecular systematics**). For several reasons, computer analysis is also an important aspect of systematics. The task of classifying all life (estimated at ten to one hundred million species) is a monumental undertaking, involving the comparative analysis of many organisms; hence, systematists have made significant use of computers to analyze large data sets and to store information so that it is easily retrievable.

paleobotany the study of ancient plants and plant communities

physiology the biochemical processes carried out by an organism

biogeography the study of the reasons for the geographic distribution of organisms

molecular systematics the analysis of DNA and other molecules to determine evolutionary relationships

Because the areas of study encompassed by systematics are so diverse, the tools or methods employed are also highly varied. One aspect of sys-

METHODOLOGICAL APPROACHES USED IN PLANT SYSTEMATICS

General Approach	Information Provided
Anatomy	Species relationships, phylogeny
Chemosystematics	Species relationships, medicinal plants
Cytogenetics	Species relationships, evolution
DNA markers	Species relationships, population genetics, evolution, phylogeny, conservation biology
Isozymes/allozymes	Species relationships, population genetics, evolution, conservation biology
Morphology	Species descriptions, phylogeny, preparation of technical keys and floras
Paleobiology	Critical information on now-extinct organisms and the evolutionary history of modern species
Palynology	Species relationships, past climates, fossil floras

tematics involves the collection, pressing, and identification of plant **specimens**, herbarium management, and archiving type specimens (the actual plant specimen upon which the name of a species is based). Some systematists are heavily involved in field research. These individuals explore many natural areas of our planet seeking to describe and catalog the diversity of life; they may also be interested in discovering potential new crops or medicinal plants. This aspect of systematics may also include the discovery and description of new species. Closely associated with this aspect of systematics is developing and refining methods of identifying plants. This is also a critical area of plant systematics that includes the writing and use of identification keys and floras.

specimen object or organism under consideration

Another important aspect of plant systematics includes the collection of evidence for determining relationships among species, that is, reconstructing phylogenies (the development of an hypothesis of evolutionary history; these are depicted as **phylogenetic** trees). Ultimately, these phylogenetic trees are used for revising classifications. Classifying organisms in a manner that reflects evolutionary history has been a longstanding goal of systematics since the work of Charles Darwin. An evolutionary biologist of the twentieth century, Theodosius Dobzhansky, stated that "Nothing in biology makes sense except in the light of evolution." Modern systematists feel that an important corollary of this famous statement is that "things make much more sense in light of phylogeny." That is, understanding the evolutionary history of organisms and their closest relatives is central to comparative biology.

phylogenetic related to phylogeny, the evolutionary development of a species

Finally, systematists are often involved in elucidating the processes of evolution. Through their study of plant diversity and natural **populations**, systematists may be involved in analyzing the levels and distribution of genetic variation within and among populations, estimating gene flow, analyzing isolating mechanisms and species origins, and investigating evolutionary mechanisms such as hybridization, **polyploidy**, and **apomixis**. As a result, one area of the broad discipline of systematics becomes intertwined with the field of evolutionary biology.

population a group of organisms of a single species that exist in the same region and interbreed

polyploidy having multiple sets of chromosomes

apomixis asexual reproduction that may mimic sexual reproduction

History of Systematics

Systematics is arguably the oldest biological discipline and has been practiced, in one form or another, for thousands of years. Prehistoric peoples knew and used almost all of the important crop plants we cultivate today, plus others specific to their geographic location. They selected plants with useful features for foods, medicines, fibers, and poisons. As civilizations developed throughout the world, people developed different ways of studying and classifying plants. Our systematics heritage traces back to early western civilizations where several men from Ancient Greece and later the Roman Empire made valuable contributions to our knowledge of plants. Theophrastus, a Greek philosopher who lived from 370 to 285 B.C.E., was a student of Aristotle and is regarded as the father of botany. Theophrastus wrote several hundred manuscripts describing and classifying plants. Many plant names used today are derived from those used by Theophrastus. In the first century A.D., Dioscorides, a Greek physician traveling with the Roman armies, wrote *De Materia Medica,* a book that described and classified more than five hundred species of plants based on their medicinal or other useful properties. This book served as the primary botanical text throughout Europe until the **Renaissance**, nearly fifteen hundred years.

Renaissance a period of artistic and intellectual expansion in Europe from the fourteenth to the sixteenth century

A fifteenth-century manuscript illumination of a marigold from Dioscorides's *De Materia Medica,* which described and classified more than five hundred species of plants based on their medicinal or other useful properties.

Hierarchical classification systems, such as those we use today, can be traced to the late 1600s and the work of Englishman John Ray. Ray developed a classification system for eighteen thousand species and introduced the concept of placing **morphologically** similar species together in a larger group, the genus. The most notable contributions during the 1600s and 1700s were those of Carl von Linné, a Swedish naturalist better known as Carolus Linnaeus. Linnaeus is considered the father of taxonomy, and is best remembered for developing the binomial system of **nomenclature**, that is, the use of a two-part name for each species; the species name consists of the genus name and the specific epithet. Linnaeus also wrote several major books, including his two-volume catalog for plant identification, *Species Plantarum*, which was published in 1753.

morphologically related to shape or form

nomenclatural naming system

All of biology, including systematics, was changed by the publication of Charles Darwin's *The Origin of Species* in 1859. Darwin's theory of evolution had an important message for systematists: Species are dynamic, changing entities, and classification is a way to order the products of evolution. Through efforts to reflect evolutionary history in classifications, we see the first evidence of phylogenetic classifications in the latter part of the nineteenth century—these are the roots of those systems in use today. Throughout the 1900s, improved means of data gathering and improved knowledge of the world's flora contributed to improvements in plant classifications. As noted, current efforts in phylogeny reconstruction are being incorporated into classifications, and systematics has expanded to include studies of speciation as well as phylogeny and classification.

Systematics and Classification

As the branch of biology concerned with understanding phylogeny and with organizing biological diversity, systematics also encompasses the development of classification systems for storage and retrieval of information. The major categories (ranks) of the botanical classification system still in wide use today are, in descending order:

Kingdom

Division (or Phylum)

Class

Order

Family

Genus

Species

Each organism can be placed into such a hierarchical system. Biological systematists attempt to create classifications that reflect phylogeny; that is, a group of closely related species will be classified into a genus; closely related **genera** are placed in a family, and so on.

genera plural of genus; a taxonomic level above species

Recent analytical developments in inferring phylogeny have improved our estimates of evolutionary history: now, in many groups of organisms, we can identify specific **lineages**, or **clades**, of related species. Unfortunately, our classification systems have not kept pace with our improved understanding of phylogeny. For this reason, clades and formal classifications

lineage ancestry; the line of evolutionary descent of an organism

clade a group of organisms composed of an ancestor and all of its descendants do not always agree. For example, many textbooks follow the Five Kingdom approach to classification of life on Earth: Kingdoms Monera, Protista, Fungi, Plantae, and Animalia. However, although this approach was a vast improvement over previous Two Kingdom classifications (Plantae and Animalia), it does not accurately reflect what we know about the history of life on Earth. Other classification systems have been proposed, some recognizing as many as eight or ten kingdoms, in an attempt to include the various major lineages of life in a classification system. At present, none of these classifications adequately meets the challenge of representing current hypotheses of the phylogeny of life. Similar inconsistencies between estimates of phylogeny and classification can also be seen at other levels of the taxonomic hierarchy; thus systematists are torn between scientific reality and the tradition of classification. This inconsistency should not be viewed as a failure of systematics; instead, it should indicate that biological systematics is a dynamic area of biology, an unending synthesis that seeks to incorporate new information into our estimates of phylogeny and our classification systems that organize biological diversity. To improve the connection between our understanding of phylogeny and classification, some systematists are attempting to develop new methods of classification. One approach is to abandon the traditional Linnaean hierarchy in favor of a strictly phylogenetic system of classification.

Systematics and Society

ecosystem an ecological community together with its environment

ethnobotany the study of traditional uses of plants within a culture

Systematics plays a key role in benefiting human society, both directly and indirectly, and has been part of the human endeavor for millennia. To understand and appreciate the extent of human impact on either local communities or global **ecosystems**, it is first critical to know what species inhabit the community or area in question. Systematists also play a major role in conservation biology and in the study of invasive species, identifying those species that are endangered by human activities, as well as those being spread by humans from one part of the globe to another. Another aspect of systematics involves the careful study of relationships of domesticated plant and animal species and their nondomesticated wild relatives. For example, determination of the closest wild relatives of a particular crop may provide new sources of genetic variation for breeding programs and crop improvement. Such research has led to significant improvements in the yield and disease resistance of many of our food plants and domesticated animals. Systematists also play a critical role in the discovery of new drugs from medicinal plants through their field work and interactions with native peoples (**ethnobotany**) who have long used these plants for medicinal purposes. Furthermore, the use of systematic knowledge of evolutionary relationships between related plant groups can guide chemists in choosing the best species to test for potential new drugs. In addition, systematists often serve as consultants to poison-control centers in hospitals because doctors need rapid and correct identifications of poisonous mushrooms, plants, and other potentially poisonous organisms. Systematists may also be involved in studying the evolution of diseases. For example, recent systematic studies have tracked the evolution of the AIDS virus and, in some instances, the pattern of transmission and source of infection.

Because systematics is such a large, diverse field, a distinction is often made among subdisciplines or subareas of endeavor. For example, plant nomenclature is the application of names to **taxa** following a strict set of published rules (the International Code of Botanical Nomenclature). Another key aspect is classification, which involves the organization of plants into groups or categories. As noted above, classification traditionally has employed the taxonomic hierarchy of categories established by Linnaeus (e.g., kingdom, division, class, etc.), but the utility of this approach to classification has recently been questioned. Some would collectively consider nomenclature and classification to represent the field of taxonomy and thus make a distinction between this and systematics, the latter focusing on the study of phylogeny and evolutionary biology. An integral part of modern systematics is phylogeny reconstruction. Phylogenetic trees showing evolutionary relationships may be reconstructed by using characters from a number of different sources, including morphological, anatomical, chemical, and palynological (pollen). Cytogenetics involves the study of chromosome **morphology**, as well as the investigation of chromosome pairing at **meiosis**. This field of systematics has enjoyed a recent revival with the application of chromosome painting techniques that facilitate the study of chromosomal evolution. Chemosystematics is the application of chemical data in a comparative fashion to study problems in systematics and to infer relationships based on the presence or absence of certain chemical **compounds** in the organisms studied. Recently, deoxyribonucleic acid (DNA) sequence data have been employed to reconstruct phylogeny, and at present serves as a major source of information to establish evolutionary relationships.

taxa a type of organism, or a level of classification of organisms

morphology shape and form

meiosis division of chromosomes in which the resulting cells have half the original number of chromosomes

compound a substance formed from two or more elements

Systematists are often broadly trained, having not only a knowledge of field biology, but also ecology, life history, plant chemistry, population biology, speciation, phylogenetics, and molecular biology. A modern systematist is often, therefore, a jack of all trades. The research of a systematist may involve field work and collection in the tropics, as well as extensive laboratory work involving DNA sequencing and gene cloning.

A fundamental goal of the field of systematics is understanding biological diversity and the organization of this knowledge into a classification system that reflects the evolutionary history of life. Hence, much of modern systematics is devoted to building evolutionary trees of relationships. The ultimate goal of this massive enterprise is the reconstruction of the "tree of life." Historically, most systematic research was based on morphological and anatomical similarities of organisms. Recently, however, the relative ease of DNA sequencing has provided another, very powerful approach to investigate relationships among species. DNA sequences and other molecular data not only are of enormous utility for inferring phylogenetic relationships, but also have other important applications. In much the same way that DNA markers can be used with human subjects to determine paternity, these same approaches can also be used for determining the parents of suspected plant and animal hybrids. This too is yet another aspect of the highly diverse field of systematics. SEE ALSO Biodiversity; Darwin, Charles; Flora; Herbaria; Identification of Plants; Phylogeny; Systematics, Molecular; Taxonomy.

Doug Soltis and Pam Soltis

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T

Taiga *See Coniferous Forest.*

Taxonomic Keys

Taxonomic keys are a written means of helping people to identify an unknown plant. Looking randomly through a flora that includes thousands of plants would take far too much time. A key provides a structure for sorting through a great deal of information, so that the user can quickly and automatically skip over many species that do not resemble the plant.

A key is written as a series of couplets. Each couplet consists of two opposing descriptions of some features of a plant. The user chooses the description that best fits the unknown plant, and is guided by that choice to another couplet or to an answer. The two halves of the couplet lead the user to different parts of the key, dealing with different subgroups of the plants included in the key. All of the plants in the half that was not chosen are instantly rejected. Because the key is constructed of pairs of contrasting choices, it is often referred to as a dichotomous key.

A taxonomic key begins by looking at large, important features that can divide the possible answers into a few large groups, thus quickly ruling out most of them. Later couplets, which divide those groups into smaller and smaller subgroups, use tiny details to help the user tell the difference between very similar species. SEE ALSO Flora; Plant Identification; Systematics, Plant; Taxonomist; Taxonomy.

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EXAMPLE OF A TAXONOMIC KEY

This is a simple taxonomic key allowing the user to identify the following common grocery store fruits: apple, banana, orange, peach, tomato, and watermelon. To use the key, pick one of these as your unknown, then read both halves of the first couplet. Which half better describes your fruit? There will be a number after that half. Go to the couplet of that number, and deal with each couplet similarly until, instead of being led to another couplet, you find the name of your fruit.

1a. Skin of fruit is thin, soft or at least flexible, edible 2
1b. Skin of fruit is thick, leathery or hard, inedible 4

2a. Seeds in several liquid-filled chambers; fruit soft throughout . . . . Tomato
2b. Seeds in hard or papery structure in center of fruit 3

3a. Seed enclosed in hard, stonelike pit; flesh soft . . . . . Peach
3b. Seeds enclosed in papery core; flesh crisp . . . . . Apple

4a. Fruit weighs more than 1 pound (0.5 kg); skin does not peel off . . Watermelon
4b. Fruit weighs less than 1 pound (0.5 kg); skin can be peeled 5

5a. Fruit long and narrow, yellow; flesh not divided into sections . . . . Banana
5b. Fruit round, orange; inner flesh divided into several segments . . . . Orange

Taxonomist

Taxonomy, or systematics, is the study of the kinds of organisms and their evolutionary history and relationships. Plant taxonomists collect and study groups of plants, focusing on the ways species arise, relationships among them, and selective forces that have molded their characteristics. To understand patterns of variation and relationships among plants, taxonomists study plants in nature, museums, laboratories, greenhouses, and experimental gardens.

Taxonomists identify, name, and classify organisms. They explore areas to collect, identify, and press representatives of every plant species, in order to record **biodiversity** before the species are lost to extinction forever. Some explorations lead to conservation efforts or to the discovery of new species, an exciting experience that presents the taxonomist with the opportunity to name and publish a description of the newly discovered species. Basic to these tasks is the challenge of developing a classification for the myriad forms of life, based on differences and similarities such as form, chromosome number, behavior, molecular structure (especially deoxyribonucleic acid [DNA] sequences), and biochemical pathways. Recent advances in cladistics have made new gains in understanding how the world's plant species are related. Cladistics is a field in which taxonomists compare the most evolutionarily relevant traits among various related organisms in addition to the most obvious ones, using computer programs.

biodiversity degree of variety of life

Taxonomists may be found working at universities, herbaria and museums, government agencies, conservation organizations, industry, and botanical gardens. Universities hire taxonomists as professors to teach and conduct research. In herbaria and museums with large plant collections, taxonomists maintain these collections, add to them, and conduct research on them. Federal and state agencies employ taxonomists in many fields, from public health and agriculture to wildlife management and forestry. Taxonomists also help prepare environmental impact statements and work with conservation and natural heritage offices. Industries that employ taxonomists include agricultural processors, pharmaceutical firms, oil companies, and commercial suppliers of plants and seeds. Most jobs in government and industry are more taxonomic and ecological than evolutionary in nature. In general, availability of these jobs depends on the training and experience of the applicant. The higher the level of preparation, the greater the responsibility and independence the job will provide.

The typical plant taxonomist will major in botany or biology with supporting work in other sciences and math. After graduating from college, the student may begin graduate training immediately to earn a M.S. or Ph.D., or work as a research assistant at a university, herbarium, or other opportunity for a year or more. Working out of doors can be very exciting and rewarding for the adventurous. Assisting an established researcher in a herbarium, laboratory, or greenhouse can be fulfilling as one learns by working with the scientist. University teaching and research offers a very stimulating mix of experiences and sometimes administrative posts.

In 1999, salaries for taxonomists ranged from $40,000 to over $80,000. Persons interested in taxonomy follow their own interests in plants, earning satisfaction from doing interesting and worthwhile work. SEE ALSO Curator of an Herbarium; Taxonomic Keys; Taxonomy.

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Taxonomy

Narrowly defined, plant taxonomy is that aspect of the study of plants having to do with taxa—that is, the naming of plant names (nomenclature) and the determination of the hierarchical relationships used to identify them or understand their relationships (identification and classification). More broadly defined, plant taxonomy includes areas of investigation from a variety of disciplines, including classification, nomenclature, phylogeny reconstruction, and investigation of evolutionary processes. Under this broader definition, the goal of taxonomy is to use comparative data to assess relationships between plants, define taxonomic boundaries between species and other ranks, provide means of identifying and communicating about the organisms, and understanding the patterns (and even the processes) in the evolution of the plants. Seen in this way, plant taxonomy overlaps and grades into the disciplines of plant systematics, **phylogenetics**, and evolution.

phylogenetic related to phylogeny, the evolutionary development of a species

Distinguishing, classifying, and naming plant taxa is basic to any study of nature and for making use of plants. To have the name of a plant (or taxon) is the prerequisite to get further information about it. Taxonomy, therefore, is inevitably necessary for all further studies of plants in order to understand their structures, life histories, and distributions, as well as for making use of them for the benefit of humans (i.e., applied botany, comprising pharmacy [medicinal plants], crops and food production [agricul-

Researchers experiment with different species of rice in an International Research Institute greenhouse in Los Banos, Luzon, Philippines.

HIERARCHY OF BOTANICAL TAXONOMIC RANKS

Rank	Suffix (or abbreviation of rank name)
domain	
kingdom	
subkingdom	
division	*-phyta, -mycota*
subdivision	(*-phytina*)
superclass	(*-phytina*) (*-phyceae, -mycetes*)
class	*-phyceae, -mycetes, -opsida, -atae*
subclass	*-idae*
superorder	*-anae*
order	*-ales*
family	*-aceae*
subfamily	*-oideae*
tribe	*-eae*
subtribe	*-inae*
genus	(usually *-us, -a, -um*)
subgenus	(subg.)
section	(sect.)
subsection	(subsect.)
series	(ser.)
species	(sp.)
subspecies	(subsp.)
variety	(var.)
forma	(fa.)

ture], forestry, production of plant raw material [fibers, gum, etc.], horticulture [ornamental plants], and conservation).

Taxonomy, therefore, is one of the oldest branches within the life sciences. But taxonomy is a synthetic science, as it uses and relies on data from all other fields of botany, including that from structural botany (**cytology** and anatomy, palynology and ultrastructure), **morphology** (including embryology), genetics (heredity), **physiology**, phytochemistry, ecology (habitats), and phytogeography (distribution of taxa).

cytology the study of cells

morphology shape and form

physiology the biochemical processes carried out by an organism

Plant Systems: Artificial and Natural

Variation among plants is not continuous—that is, there are discontinuities separating one type of plant from another. We distinguish different individuals of the same kind, and we distinguish different kinds of oaks, roses, dandelions, violets, and so on. Variations among taxa are of different quantity and quality, and as a result, they can be arranged in a hierarchical system. Those plants being almost alike and interbreeding belong to the same species. All similar species together form a genus, similar **genera** are put together as a family, and so forth. The tasks of taxonomy, therefore, are to describe the plants thoroughly (phytography) and to compare them in order to discover natural groups, and to classify (classification) and name them (nomenclature).

genera plural of genus; a taxonomic level above species

Other questions examined in evolutionary botany and phylogenetics include: How did the differences between taxa come about? And what are the reasons for their mutual hierarchical connections? To some authors, all these studies together are called (biological) systematics, and taxonomy is restricted to dealing only with classification.

INTERNATIONAL CODE OF BOTANICAL NOMENCLATURE (ICBN)

In order to standardize terminology and promote effective communication among plant scientists, plant taxonomists have agreed to a set of formal guidelines to be used when naming plants. Known as the International Code of Botanical Nomenclature (ICBN), these guidelines were adopted in 1867 and serve as the official reference rules with which nomenclatural decisions about plants must be made. The Code is updated and modified periodically by an international committee on plant nomenclature and serves as the basis for all naming of plant ranks from infraspecific taxa (variety, subspecies, etc.) to species and to taxa of higher ranks (genus, family, order, etc.). There is also a separate code for the naming of cultivated plants, which has nomenclatural conventions very similar to that of the ICBN.

At its founding, the ICBN agreed that plant nomenclature would officially begin with the work by Linnaeus, *Species Plantarum,* published in 1753. To avoid unnecessary duplication of names for the same species or to stabilize the way plant names are applied to the various taxonomic hierarchies, a system of date priority was also instituted, so that the earliest correctly published name for a taxon must be used if the plants concerned are found to be the same. Taxonomic publications describing new species or proposing new genera, families, or other formal ranks are expected to follow the rules included in the ICBN. If these requirements are not met, the name proposed by the botanist may be rejected.

The Swedish botanist Carolus Linnaeus (1707–1778) was an excellent analytical observer, and his talent for methodical recording, concise summarizing, and systematic thinking enabled him to produce a synthesis, the Linnaean System, which was in use for almost one hundred years. It was easy to handle because it was mainly based on very few numerical flower characters (number of stamens and styles). A system using only one or very few characters is considered an artificial one, and the Linnaean System for the most part did not reflect natural (evolutionary) relationships.

Botanists who followed Linnaeus elaborated a natural system of classification, considering all organs of the plant. Important contributors included the Frenchmen M. Adanson, A. L. de Jussieu, and Jean Baptiste de Lamarck; their Swiss colleagues A. P. and Augustin de Candolle; the Scot Robert Brown; the Austrian S. Endlicher; and the Britons G. Bentham and J. D. Hooker. Their system was based on comparative morphology, a discipline arising in the beginning of the nineteenth century. It made use of the concept of **homology** and of crucial discoveries like the alternation of generations by the German W. Hofmeister. Their "natural system"—though subsequently modified in many ways—essentially persisted up to modern times, although it aimed at reflecting the natural order they believed to have been established by God the Creator rather than attempting to reveal evolutionary relationships.

Biological Kinship: Phylogenetic, Phenetic, and Evolutionary Systems

A revolution in biology was the discovery of evolution and its mechanisms by the English naturalists Charles Darwin and A. R. Wallace in the middle of the nineteenth century, presenting common descent and gradual changes in geological time scale as an explanation for the taxonomic hierarchy already established. No essential changes of the previous morphologically based system, therefore, proved necessary. However, the acceptance of evolution as a unifying concept in biology turned the attention of taxonomists to questions of ancestry and descent.

Toward the end of the nineteenth century, the connections among taxa were more carefully studied in order to answer the questions: Which are the older (i.e., more primitive) characters and taxa, and which are the younger and more advanced ones? How did specific adaptations evolve? A typical and important question concerned the evolution of pollination mechanisms. Are unisexual wind-pollinated flowers primitive (original) or advanced (derived, secondary) or vice versa?

The first attempts to answer these questions were by A. Engler and R. V. Wettstein and followers in the late nineteenth century. They considered the *Fagales* (beech and birch families), *Juglandaceae* (hickories), and *Salicaceae* (willows and cottonwoods) as the most primitive angiosperms because of their small, wind-pollinated, unisexual flowers arranged in **catkins**, thus forming a presumptive link between the more ancestral gymnosperms (including conifers like pines, spruces, firs, cedars, etc.) and the **angiosperms**, which often have showy, insect-pollinated, hermaphroditic flowers. However, subsequent research in the early part of the twentieth century, especially by C. E. Bessey, showed that the phylogenetic relations are just the other way around: angiosperms appear to be primarily hermaphroditic and insect-pollinated, these traits being

Pussy willow (*Salix discolor*) catkins are pollinated by the wind, dispersing their spores. Though *Salicaceae* (willows and cottonwoods) were once considered the most primitive angiosperms, subsequent research has shown that the catkin-bearing families evolved later, adapting to habitats in which wind pollination is advantageous.

responsible for one of their major advantages (more effective pollination) in contrast to **gymnosperms**. The catkin-bearing families are judged to have evolved later, adapting to habitats in which wind pollination is advantageous.

In the beginning of the twentieth century, the new field of genetics strongly improved our understanding of evolution. Many phylogenists, however, were skeptical because of the large number of empirically ill-based, speculative phylogenetic trees produced at the turn of the century. Toward the middle of the twentieth century, taxonomy at the specific and infraspecific (below species) levels was changed into the New Systematics, Biosystematics, and Experimental Systematics, strongly accelerated by knowledge from genetics, population genetics, breeding systems, cytogenetics, karyology (chromosome number), and ecology in combination with traditional data from morphology, embryology, anatomy, and distribution.

homology a similarity in structure between anatomical parts due to descent from a common ancestor

catkin a flowering structure used for wind pollination

angiosperm a flowering plant

gymnosperm a major group of plants that includes the conifers

Despite these stimulating and largely successful efforts to combine understanding of evolutionary processes with the needs and challenges of taxonomy, the study of phylogeny (trees of evolutionary descent) and of systematics above the species level (macrosystematics) was not markedly improved because no data were available for establishing scientifically sound hypotheses. A pragmatic method was developed, therefore, that tried to overcome the difficulty of having classification based on phylogeny, but these were often burdened with intuitive and speculative hypotheses. Phenetic systems were designed in the late 1950s to resolve these problems.

Phenetics

Phenetics is a strictly empirical method. It avoids evaluating character states as ancestral versus derived and thus avoids any phylogenetic hypotheses. All characters are treated as equal (unweighted). The use of newly developed mathematical methods and of electronic data processing allowed calculation of large amounts of character data and classification based exclusively on overall similarity. The resulting phenetic system does not attempt to reveal kinship (relationships based on descent). As it is not biased by phylogenetic judgements, it can be considered, in some way, a multipurpose system allowing a maximum of predictability. Convergences (i.e., similarities caused by evolutionary adaptation to the same environmental factors), however, may not become apparent in a phenetic system.

Not all workers were satisfied with phenetics, however, and starting in the late 1960s the method called cladistics was developed for handling taxonomic characters and exploring relationships between taxa. Cladistics, which was strongly opposed to phenetics, developed rapidly and successfully.

Cladistics

entomologist a scientist who studies insects

Using and developing the ideas and concepts of the German **entomologist** Willi Hennig, cladistics is an effective tool for studying and describing phylogenetic relationships and reconstructing a truly phylogenetic system. It constructs conceptually strict phylogenetic branching patterns by evaluating character states as ancestral (plesiomorphic) or derived (apomorphic). The basic assumption is that speciation takes place mainly by bifurcation: one ancestral species splits into two sister species, which are to be treated as having equal taxonomic rank, both characterized by newly developed (apomorphic) characters.

paraphyletic group a taxonomic group that excludes one or more descendants of a common ancestor

monophyletic a group that includes an ancestral species and all its descendants

The big advantage of cladistics is the use of clear assumptions and procedures, in contrast to intuitive phylogenetic trees devised by earlier generations of phylogenetic taxonomists. An important conceptual change is the more restrictive definition of monophyly, meaning a group containing all descendants of a certain taxon. But if, say, one or more descendants are excluded, the remaining group forms a **paraphyletic group** because it does not contain all descendants from the common ancestor. In pre-cladistic phylogenetic systems, however, a paraphyletic group has been accepted as being **monophyletic** because all its members share a common ancestor. This, however, has not been accepted by cladistic practitioners.

These simple concepts, seemingly formalistic and of no empirical value, have, however, major effects on defining phylogenetic taxa and constructing a phylogeny-based system. Through this type of work, the understanding of relationships in the plant kingdom has recently undergone a major revision.

clade a group of organisms composed of an ancestor and all of its descendants

There is much evidence, accumulated for many decades and including modern molecular investigations, that all plants in the strict sense (the so-called *Embryophyta*, the bryophytes and the vascular plants) are offspring of the green algae (*Chlorophyta* s.l.) because they share a combination of common features that would have been unlikely to have evolved several times independently. Both together form a single big branch (**clade**) of the phylogenetic tree and, therefore, are united into one monophyletic taxon, the *Chlorobionta*. This big and highly heterogenous taxon, comprising unicellular algae together with all the land plants, has the same rank in the phylogenetic system as the red algae, comprising a number of seaweeds only. In a cladistic sense, you cannot unite the green algae with the red algae (and other algal groups) to form the taxon algae. Such a group, which mixes organisms from different branches, is called a polyphyletic group. SEE ALSO ALGAE; BESSEY, CHARLES; CANDOLLE, AUGUSTIN DE; FAMILY; FLORA; HERBARIA; HOOKER, JOSEPH DALTON; IDENTIFICATION OF PLANTS; LINNAEUS, CAROLUS; PHYLOGENY; SPECIES; SYSTEMATICS, MOLECULAR; SYSTEMATICS, PLANT; TAXONOMIC KEYS; TAXONOMIST.

Manfred A. Fischer

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Taxonomy, History of

The origin of plant taxonomy goes back centuries, and there are thought-provoking parallels between folk classifications and those produced in more recent times. The Swedish botanist Carolus Linnaeus (1707–1778) provided the first widely used framework, the basis of our current classification. He placed all plants in a genus and species, giving each a **binomial** (such as *Taraxacum officinale* for the dandelion), allowing botanists worldwide to communicate.

binomial two-part

Linnaeus was not very successful in recognizing larger groupings of plants, but in 1786 Antoine-Laurent de Jussieu put all **genera** in families. Jussieu believed that nature could be represented as a single, continuous series of relationships, and he made his families (and genera) of convenient sizes. There was much debate during the ensuing century and a half as to whether all characters should be used in classification or only in the most important ones. The issue was never resolved, but in practice the human mind cannot compute relationships using all characters. Another issue was less contentious: It had been realized that prominent characters used for the identification of plants (in keys) might be different from the most fundamental ones used in deciding on the same plant's relationships.

genera plural of genus; a taxonomic level above species

The Nineteenth Century

The late eighteenth and the nineteenth centuries saw many new developments in the area of plant taxonomy. Voyages of discovery and colonization yielded a stream of unknown plants needing names. Plants of economic importance like quinine, breadfruit, rubber, and tea were moved to colonies where they could best be exploited. Herbaria, collections of flattened and dried plants attached to paper, were developed. By the middle of the nineteenth century most large herbaria such as those at Washington, D.C., Kew (London), and Paris were owned by the state or, less frequently, universities. Systematic work was largely based on the dried plants there, with botanical gardens or field studies being of less importance. This practice persisted through much of the twentieth century.

Darwin's ideas on evolution, published in 1859, had little effect on the practice of taxonomy, although many workers used the ideas to explain the classifications they produced—using techniques very similar to those of Jussieu. Systematists like Asa Gray were among Darwin's staunchest supporters. Darwin himself was very interested in genealogies, ancestor-descendant sequences. Most botanists thought that without fossils such genealogies could not be recognized, but nonetheless when they talked about relationships it was most often in terms of living group A giving rise to living group B—just as if they were talking about genealogies.

Along with professional taxonomists, there was a flourishing group of amateurs. Botany was particularly popular among women. In the later nineteenth century, first in Germany and later in the United States, reaction against classificatory botany set in. **Physiology**, anatomy, ecology, and the study of lower plants were thought to be more exciting, particularly among those who worked at universities. Charles Bessey was a forceful proponent of this "new Botany" in the United States, and although he was not particularly against taxonomy, the popularity of the new approach led to a decline in the status of taxonomic botany and of taxonomists. In the sometimes bitter arguments, taxonomic botany was often portrayed as an old-fashioned subject practiced by women and children and of no scientific interest.

physiology the biochemical processes carried out by an organism

In the 1930s emphasis came to be placed on the study of living plants both in the wild and the greenhouse, particularly in the area of species and speciation. G. Ledyard Stebbins, one of the most influential botanists of his time, was a founder, along with Ernst Mayr, Gaylord Simpson, and others, of the "evolutionary synthesis," an integration of evolutionary theory, systematics, and **morphology**. However, taxonomists working in herbaria—where most taxonomic work was still carried out—were little affected by such developments.

morphology shape and form

Since the late nineteenth century, new disciplines such as anatomy, **cytology**, and plant chemistry had been promoted as likely to solve the difficult problem of understanding the limits and relationships of groups like genera and families. Progress, however, was painfully slow. In the latter part of the twentieth century, a system of relationships that built on those of earlier works was proposed by Arthur Cronquist.

cytology the study of cells

Phenetics and Cladistics

However, changes were afoot. In the 1960s phenetics, or numerical taxonomy, was very popular. By looking at many characters and using early computers to analyze the data, botanists hoped to produce classifications of maximum usefulness, stability, and objectivity. Such botanists were less interested in evolutionary relationships, and problems became evident both in the goals of phenetics and in some analytical techniques. Nevertheless, many of their techniques remain useful, particularly when working at the level of species. In the late 1970s the cladistics approach of Willi Hennig became widely known, and this led to the development of new ways of producing treelike diagrams depicting hypothesized **phylogenetic** relationships. In such phylogenies, genera and species were not linked directly but by way of their common ancestors. After much debate, Hennig's principles, somewhat modified, have been accepted by most botanists, allowing taxonomists to justify their work much more clearly.

phylogenetic related to phylogeny, the evolutionary development of a species

In the 1990s the advent of molecular techniques, combined with the practice of phylogenetic analysis and the use of computers, led to a rapid improvement in our understanding of relationships among the main groupings of plants. This has become perhaps the most common kind of systematic work in universities and is notable for being highly collaborative, contrasting with the individuality of classic taxonomic work. Studies on **biogeography**, evolution, and diversification have been greatly facilitated as a result. However, morphological studies have tended to stagnate, and there has been relatively little emphasis on studies at the species level. Furthermore, interest in conservation and **biodiversity** has made it clear how little we understand about most species that have been described, how many species—particularly in groups like fungi—remain to be described, and how

biogeography the study of the reasons for the geographic distribution of organisms

biodiversity degree of variety of life

few systematists remain engaged in this kind of work. SEE ALSO Bessey, Charles; Britton, Nathaniel; Candolle, Augustin de; Gray, Asa; Linnaeus, Carolus; Phylogeny; Taxonomic Keys; Taxonomist; Taxonomy; Torrey, John.

Peter F. Stevens

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Tea

In the broadest sense, tea is a water extract of leaves, blossoms, roots, bark, or other parts of plants. The extraction can be done by soaking, boiling, and steeping (soaking in water below the boiling point). The extract can be an ordinary beverage or a medication.

The most common tea is from the leaves of the plant known as *Camellia sinensis*. Chinese legend attributes the accidental discovery (around 2700 B.C.E.) of drink made from this plant to King Shen Nong, who noticed tea leaves had blown into his kettle of boiling water. The tea that Shen Nong most probably drank is green tea, which quickly became the most popular beverage in China, Japan, Korea, and the countries of Southeast Asia. (Its popularity has continued, and in fact, tea brewed from *Camellia sinensis* is second only to water as the world's most popular beverage.) Unlike orange pekoe (a black tea, which is most identified as tea by consumers in the United States), fresh green tea beverage is tinted apple green, hence its name. Other teas from *Camellia sinensis* are broadly termed black, red, and yellow according to the appearance of either the dried leaf or its extract.

Tea Processing

All *Camellia sinensis* teas are from the growing ends and buds (called the flushes) of the tea tree or shrub. Flushes that undergo a process called fermentation become black, red, or yellow teas. This process is not the one in

Workers harvest tea leaves on a plantation in Assam, India.

TEN LARGEST TEA-PRODUCING AND EXPORTING COUNTRIES, 1998

Principal Producers	Quantity Produced (in metric tons)	Quantity Exported (in metric tons)
India	870,400	225,000
China	687,675	219,325
Kenya	294,165	263,685
Sri Lanka	280,056	267,726
Indonesia	152,063	67,219
Turkey	120,300	17,526
Japan	91,000	752
Myanmar	66,808	N/A
Vietnam	51,000	33,000
Bangladesh	50,575	25,049

SOURCE: Food and Agriculture Organization of the United Nations.

enzyme a protein that controls a reaction in a cell

antioxidant a substance that prevents damage from oxygen or other reactive substances

which microbes are added to make alcohol-containing beverages, cheese, sauerkraut, and other foods. Rather, an **enzyme** (catalyst) changes molecules called polyphenols that are green into more complex polyphenols that are red and yellow. Both the enzyme and the polyphenols are in (and not added to) the tea leaf, and leaf fermentation is activated first by withering (slow drying of the leaves) and then by rolling (pressing the leaves so that the sap comes to the surface). Black tea is made when the fresh tea leaves are allowed to totally ferment (100 percent). Partial fermentation of 10 to 15 percent and 20 to 30 percent yields yellow and red (sometimes known as oolong) teas, respectively. Steaming or roasting the leaves to inactivate the enzymes soon after harvest prevents fermentation, and these are the first steps in green tea manufacture.

Health Benefits

Tea has been called an elixir of life and is commonly used as an antidote to mental fatigue. This effect may in fact be caffeine-induced. Although there is less in tea than in coffee, enough caffeine is present in a cup of tea to dilate the brain's blood vessels. Tea seems to have a wide range of health benefits, as a survey of the scientific literature between 1998 and 2000 attests. The two principal active ingredients are the tea polyphenols (a group of six chemically and structurally related molecules) and theanine (an unusual amino acid found in green but not black tea beverage). (Amino acids are the building blocks of proteins.) Like vitamins C and E, the tea polyphenols are **antioxidants** that may slow the onset of atherosclerosis, some forms of cancer, and the onset and severity of arthritis. Nonantioxidant properties of tea polyphenols also may contribute to their overall effectiveness in disease prevention. Evidence is mounting to suggest theanine can help anticancer chemicals (such as doxorubicin) kill tumor cells more specifically, but how it does this is still unknown.

Economic Importance of Tea

Worldwide tea production was over 3 million metric tons (worth about $8 billion to growers) in 1998. India and China produced about half of this output, most of it for internal consumption. Whereas China and Japan produce mainly green and partially fermented teas, the other growers supply mainly black teas. The world's largest importers of tea are the United King-

TEN LARGEST TEA-IMPORTING COUNTRIES, 1998

Principal Consumers	Quantity Imported (in metric tons)
United Kingdom	175,829
Russian Federation	150,225
Pakistan	111,559
United States	96,646
Egypt	65,457
Japan	45,442
Iran	40,000
Germany	38,664
Poland	36,569
Sudan	23,843

SOURCE: Food and Agriculture Organization of the United Nations.

dom, the Russian Federation, Pakistan, and the United States. However, Ireland, the United Kingdom, Turkey, Syria, and Iran are the world's leading consumers on a per-capita basis.

The estimated wholesale value of the U.S. tea industry has risen from $1.84 billion in 1990 to $4.60 billion in 1999 and continues to rise, according to the U.S. Tea Association. The largest segment of that growth was due to the increased consumption of ready-to-drink teas, which rose from $0.2 billion to $1.65 billion dollars during this period.

Herbal Tea

Herbal teas, like regular tea, have been consumed for eons and for the same calming, stimulating, or medicinal reasons. Tea made from chamomile flowers steeped for more than thirty minutes in boiling water is said to be a sedative that also soothes indigestion. Tea made from the rootstock of comfrey was believed to heal broken bones and be a good gargle for sore throat and cure bleeding gums. Tea made from sassafras root bark or leaves may have the pleasant taste of root beer but will cause the drinker to perspire and urinate. This tea has been used for everything from a blood-thinner to a cure for rheumatism and syphilis. Indeed, teas can be made from many plants and may contain thousands of active **compounds**. The U.S. Food and Drug Administration recommends that herbal tea drinkers use caution. Chamomile can cause a severe allergic reaction in people with sensitivity to ragweed, asters, or chrysanthemums. Liver disease has been reported in drinkers of large amounts of comfrey tea (ten or more cups a day), and comfrey contains a chemical that causes cancer in rats. The major chemical components of sassafras tea, once used to flavor root beer, were banned thirty years ago because they caused cancer in rats. The use of caution means moderation—daily consumption of any particular herbal tea for not more than two to three days at a time—and avoidance—by children, pregnant women, or nursing mothers. SEE ALSO COFFEE; ECONOMIC IMPORTANCE OF PLANTS; HERBALS AND HERBALISTS; HERBS AND SPICES; MEDICINAL PLANTS.

Robert Gutman

compound a substance formed from two or more elements

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Terpenes

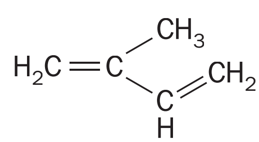
compound a substance formed from two or more elements

hemiterpene a half terpene

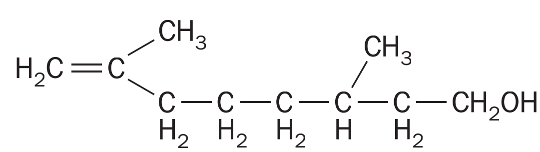
pigments colored molecules

carotenoid a colored molecule made by plants

Terpenes (terpenoids) are a very large family of plant **compounds** that play a variety of roles in many different plants. All terpenes are constructed from isoprenoid units by biochemically unusual pathways involving highly reactive intermediates. The **hemiterpene** isoprene, which contains five carbons (one isoprene unit), is a gas emitted into the atmosphere by many plant species, where it plays a role in the chemistry of ozone production. A monoterpene (monoterpenoid) contains ten carbons (two isoprene units); a sesquiterpene, fifteen carbons (three isoprene units); a diterpene, twenty carbons (four isoprene units). Triterpenes (thirty carbons) are important structural components of plant cell membranes. Many plant **pigments**, including the yellow and red **carotenoids**, are tetraterpenes (forty carbons). Natural rubber is a polyterpene containing many isoprene units. The monoterpenes and sesquiterpenes are common components of the essential oils of herbs and spices (peppermint, lavender), of flower scents (rose), and of turpentine derived from the resin of evergreen trees.



Isoprene



Citronellol, a monoterpene

The bark on a Western yew tree in Washington's Mount Rainier National Park. The cancer-fighting drug taxol was first isolated from yew bark.

These compounds have important uses as flavorings and perfumes, as well as intermediates in the production of other commercial products like solvents and adhesives. Many terpenes play roles as plant hormones and in the chemical defenses of plants against microbial diseases and insect **herbivores**; many others have important medicinal properties. Artemisinin is a sesquiterpene drug derived from traditional Chinese herbal medicine that is useful for treating malaria, and taxol obtained from yew trees is a diterpenoid that is highly effective in treating cancer. Recent advances in molecular biology have made it possible to genetically engineer terpene metabolism in plants for agricultural, industrial, and pharmaceutical purposes. SEE ALSO Atmosphere and Plants; Flavor and Fragrance Chemist; Hormones; Medicinal Plants; Oils, Plant-Derived; Pigments; Poisonous Plants.

herbivore an organism that feeds on plant parts

Rodney Croteau

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Tissue Culture

For a variety of purposes, plant cells, tissues, organs, and whole plants can be grown in labware containing a medium composed of defined molecules. Tissue culture media provide water, minerals, vitamins, hormones, carbon sources, and antibiotics depending on the plant material being cultured. Since most living plant cells are **totipotent,** scientists can manipulate the medium to regenerate whole plants from even a single genetically engineered plant cell or from a cluster of cells from a rare plant. Hormones in the medium determine what plant parts form from the cells (callus) in the culture: Auxins stimulate root formation and cytokinins stimulate shoot formation. The medium may contain agar, agarose, phytagel, or other **polysaccharides** to form a semisolid gel to support the plant tissue. The container must be colorless if photosynthesis is to be supported, and the light source should not be too intense to avoid the greenhouse effect inside the container. If the container is not ventilated, a carbon source such as sucrose will have to be used. Tissues must be subcultured periodically to avoid **solute** concentration buildup if the container is ventilated. Antibiotics may be used to keep the culture clear of bacteria, fungi, or other contaminants or to select for genetically engineered cells. Tissue culture techniques are also used to generate large numbers of genetically identical plants for agricultural applications, or to generate additional plants of rare or endangered species. SEE ALSO Genetic Engineering; Propagation; Reproduction, Asexual; Transgenic Plants.

totipotent capable of forming entire plants from individual cells

polysaccharide a linked chain of many sugar molecules

solute a substance dissolved in a solution

Ross Koning

A petri dish of Venus's-flytrap tissues.

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Tissues

Plants are a composite of cells organized into tissues. Every cell within these tissues has a unique size and shape and is surrounded by a wall composed of a complex carbohydrate called cellulose. Plant cells are attached to each other by a gluelike substance, pectin, that cements them together.

All plant tissues originate in meristems, which are unique tissues of the plant body. They are the sites of new cell production and of the genetic events necessary for cellular specialization. Meristems can be categorized by their locations. **Apical meristems** are composed of groups of dividing cells at the tips of shoots (branches) and roots. When meristematic cells produced by apical meristems begin elongating, they are classified as primary meristems. There are three types of primary meristems: protoderm, ground meristem, and procambium. As primary meristem cells stop dividing and begin differentiating, their classification changes to primary tissues. There are four primary tissues: the epidermis derived from protoderm, the ground tissues (parenchyma, sclerenchyma, and collenchyma) derived from ground meristem, and two types of vascular tissue—xylem and phloem—derived from procambium. Primary tissues have specific positions in the plant body and specific functions.

apical meristem region of dividing cells at the tips of growing plants

As the organs of the plant body age, the stems and roots often grow wider. Growth in width is called lateral growth and is initiated by secondary meristems. There are two types of secondary meristems: the vascular cambium and the cork cambium. The vascular cambium is located near the outside of stems and roots. Its function is to produce new cells that become part of the secondary xylem and secondary phloem tissues. The cork cambium is located near the outer edge of older stems and roots, and it produces the periderm, which is part of the bark.

The Concept of the Tissue System

In 1875, German scientist Julius von Sachs introduced a scheme that is still used today: the tissue systems. A tissue system is composed of tissues with a common position and function. The plant body has three tissue systems: dermal, ground, and vascular.

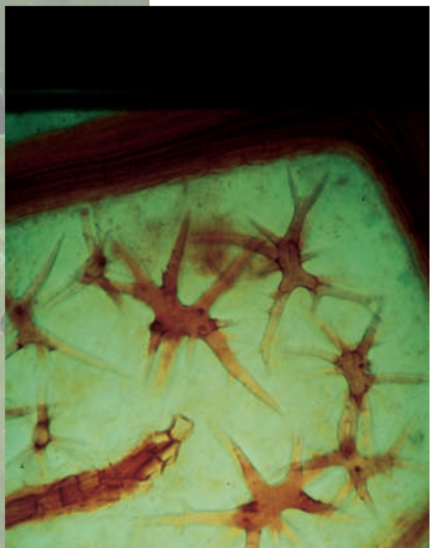
The dermal tissue system forms the outer, protective covering of the plant body. In young plants, the dermal tissue system consists of epidermis tissue. In some plants and plant organs, the epidermis remains intact

PLANT TISSUE SYSTEMS

Tissue System	Tissue	Meristem Origin	Primary or Secondary?	Function
Dermal	Epidermis	Protoderm	Primary	Protect against pathogen entry and inhibit water loss
	Periderm	Cork cambium	Secondary	Protect against pathogen entry and inhibit water loss
Ground*	Parenchyma	Ground meristem†	Both	Storage of food products and water, photosynthesis, and other basic processes
	Collenchyma	Ground meristem	Both	Structural support of leaves and young stems
	Sclerenchyma	Ground meristem	Both	Structural support of plant organs
Vascular	Xylem	Procambium and vascular cambium	Both	Movement of water and dissolved materials throughout the plant
	Phloem	Procambium and vascular cambium	Both	Movement of sugars throughout the plant

* The gound tissues are located mostly in the cortex and pith of stems, roots, and fruits and in the mesophyll of leaves.

† These tissues can also appear as component parts of other complex tissues, e.g., parenchyma cells are an important part of the xylem.



A *Trochodendron* leaf whose tissues have been cleared to reveal the elaborate sclereids.

throughout the life of the plant. However, in some aging plants the epidermis is torn and an underlying secondary meristem, the cork cambium, produces a secondary tissue, the periderm. The periderm, which consists of stacks of cells with waxy cell walls, then takes over the protective function. Although both the epidermis and the periderm occupy the same outer position and perform the same protective functions, they are derived from different meristems.

The ground tissue system consists of tissues that are produced by the ground meristem, one of the primary meristems. It is responsible for functions such as photosynthesis and storage and is comprised of the following tissues: parenchyma, collenchyma, and sclerenchyma.

The vascular tissue system is composed of the water- and mineral-conducting tissue, xylem, and the food-conducting tissue, phloem. Primary vascular tissue is produced by the primary meristem, procambium, and secondary vascular tissue is produced by the vascular cambium.

The Ground Tissue System

The ground meristem produces the primary ground tissue of stems, leaves, roots, flowers, and fruits. The three ground tissues are parenchyma, collenchyma, and sclerenchyma. In stems and roots, ground tissues are located in the cortex and pith. The cortex lies between the epidermis and vascular tissue; the pith, when it is present, is located in the center of the organ. In leaves, the ground tissue is called mesophyll and is located between the upper and lower epidermis.

Parenchyma Tissue. Typically the cortex of roots, the pith of stems, the mesophyll of leaves, and the edible parts of fruits are composed entirely of parenchyma tissue. Although parenchyma cells making up this tissue vary in size, shape, wall structure, and function, generally they are living at maturity, are **polyhedral** in shape, have thin cell walls, and perform many of the basic physiological functions of the plant. Parenchyma tissue in the cortex and pith regions of roots and stems are often specialized for storage of carbohydrates, proteins, fats, and oils. Water is stored in the mesophyll of **succulent** plants. Cells in the mesophyll of leaves contain **chloroplasts** and are specialized for photosynthesis. There are two types of leaf mesophyll: palisade mesophyll is composed of columnar-shaped cells near the upper surface of the leaf, and branched spongy mesophyll is next to the lower surface.

polyhedral in the form of a polyhedron, a solid whose sides are polygons

succulent marked by fleshy, water-holding leaves or stems

chloroplast the photosynthetic organelle of plants and algae

Collenchyma Tissue. Collenchyma is a supporting tissue found in the leaves and young stems. This tissue provides strong but flexible support. Collenchyma cells are living at maturity and have plastic walls that can expand with the growing organ. Collenchyma cells are elongated and have a thick cell wall containing large amounts of pectins and water. The unevenly thickened cell wall is a definitive feature of collenchyma cells. Strands of collenchyma tissue often occur just beneath the epidermis in stems and petioles and between vascular bundles and the epidermis in leaves.

Sclerenchyma Tissue. Sclerenchyma is also supporting tissue, but its cells are generally dead at maturity. Sclerenchyma cells have thick cell walls that are usually lignified. Lignin is a complex **polymer** that is impervious to water. Supporting sclerenchyma tissue is common in plant organs that have completed elongation growth. Lignification of the cell walls of sclerenchyma

polymer a large molecule made from many similar parts cells not only makes them harder and stronger, it also makes them resistant to decay. There are two major categories of sclerenchyma cells: sclereids and fibers. Generally sclereids are short and irregular in shape, while fibers are long and narrow. Sclereids often have massively thick lignified cell walls. Columnar-shaped sclereids form the outer seed coat tissue of bean seeds; clusters of sclereids give pear fruits their gritty texture; branched sclereids are sometimes present in the mesophyll of leaves; and strands of elongate fibers are important structural components in the cortex, associated with vascular tissue, or extending from vascular bundles to the epidermis in leaves. Extremely long fibers from flax and ramie plants, and other plant species, are commercially important sources of fibers used in the manufacture of ropes and fabrics.

Cross-section of a three-year-old elderberry (*Sambucus*) stem. The vascular cambium is visible at the boundary between the greenish phloem and the brownish secondary xylem. The cork cambium is just inside the dark cells at the stem surface.

The Dermal Tissue System

The dermal tissue system consists of the epidermis and the periderm. The epidermis is a primary tissue derived from the protoderm, and the periderm is a secondary tissue derived from the cork cambium.

The Epidermis. The epidermis is a complex tissue and is the outermost covering of the primary plant body. It provides a protective barrier between the internal tissues of the plant and the outside. Although the epidermis is generally one cell layer thick, it is made up of several different cell types. From the surface, epidermal cells appear slightly elongated in stems and leaf petioles and irregular in outline like jigsaw puzzle pieces. Epidermal cells generally lack chloroplasts and their outer surfaces are covered by a waxy layer, the **cuticle**. The cuticle reduces water loss from the plant surface. Another common epidermal cell type, the guard cell, contains chloroplasts. Guard cells are always present in pairs surrounding a pore. A pair of guard cells and its pore is called a stoma (plural, **stomata**). The exchange of gases essential for photosynthesis, such as the uptake of carbon dioxide, and the loss of water vapor through **transpiration** occur through stomata. Stomata are common in photosynthetic leaves and other photosynthetic organs, such as herbaceous stems and aerial roots. In many plants, stomata are surrounded by cells that differ from ordinary epidermal cells; these are called subsidiary cells. Another common type of epidermal structure is the trichome. Trichomes may be single-celled outgrowths, such as root hairs, or they may be simple or complex multicellular structures.

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss

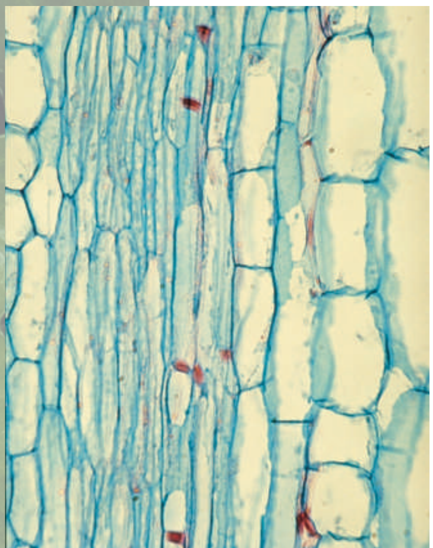
stomata openings between guard cells on the underside of leaves that allow gas exchange

transpiration movement of water from soil to atmosphere through a plant

The Periderm. The periderm forms the outer covering over most older stems and roots. It may have a few to several cell layers. During the first year of secondary growth, the cork cambium produces tabular-shaped cork cells to the outside, and the epidermis is crushed and destroyed. Additional cork cambia may arise deeper within the plant body in subsequent years. In some plants, cylinders or arcs of cork cambia activate, resulting in multiple layers of periderm tissue. Suberized (waxy) cork cells form an impervious outer plant tissue.

The Vascular Tissue System

Xylem and phloem are complex tissues comprising the vascular tissue system. Vascular tissue is present in all stems, roots, leaves, flower parts, seeds, and fruits.



Cucumber (*Cucurbita*) stem section. Strands of phloem are shown in at the center; the cells have red-stained end walls.

Xylem Tissue. Xylem is a complex tissue specialized to transport water and dissolved minerals. In young organs, xylem is formed from a primary meristem, the procambium, and is a primary tissue. In older stems and roots it continues to form as a secondary tissue from a secondary meristem, the vascular cambium.

The two cell types specifically charged with water transport are vessel members and tracheids. These cell types are fundamentally similar in that both are dead at maturity and tend to have thickened cell walls with openings called pits. A pit is a thin region in the wall that extends between two adjacent cells. Pits allow water to pass freely, but air bubbles are trapped. Differences are apparent in the end walls of these cells. The end walls of tracheids are tapered and cells connected end-to-end communicate through pits. The end walls of vessel members are completely open. The open area is called a perforation plate. When two vessel members are connected end-to-end they form an open tube called a vessel, which is typically composed of several vessel members connected end-to-end. The end walls of vessel members at opposite ends of a vessel have non-perforated end walls, so a vessel is like a length of tube with closed ends. The non-perforated end walls do have pits, allowing water and minerals to easily pass from one vessel to another, but restricting air bubbles to a single vessel. Because air bubbles block the movement of water, any that form inside tracheids and vessel members create conducting problems. Isolating air bubbles and restricting their movement improves conducting efficiency of tracheids and vessels.

Xylem is composed of several different cell types. In addition to vessel members and tracheids, parenchyma cells and fibers are commonly found in xylem tissue. Parenchyma cells and fibers contribute to the transport and support function of this tissue.

Phloem Tissue. The complex phloem tissue transports sugars from leaves to the other plant organs. It is a primary tissue in young organs, and in older stems and roots it is a secondary tissue formed from the vascular cambium.

Within phloem tissue, cells that collect and transport sugars are called sieve-tube members (STMs). STMs are living cells joined end-to-end to form a tubelike structure called a sieve tube. Each STM has a unique attachment to another important phloem cell type called a companion cell. Companions cells help regulate cellular functions inside STMs and assist in loading and unloading sugars into STMs. Other cells in the phloem include parenchyma cells and fibers. Fibers act to strengthen and support the weight of the phloem and surrounding tissues, and phloem parenchyma cells store water and help with loading and unloading sugars. SEE ALSO Anatomy of Plants; Cells, Specialized Types; Meristems; Sachs, Julius von; Vascular Tissues.

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Tobacco

Tobacco, *Nicotiana tabacum* (family Solanaceae), is grown in over one hundred countries around the world, in both temperate and tropical climates. It is a stout, rapidly growing annual, 1 to 2 meters tall. It has large, ovate to oblong leaves and produces numerous white-pinkish flowers with corollas about 2 centimeters long. Tobacco seeds are minute, so in commercial production seedlings are generally produced in plant beds or in greenhouses and transferred to the field. Production and harvesting methods differ widely depending on the type of tobacco being produced, but most tobacco types require significant inputs of time, labor, and pest management. Both underfertilization and overfertilization may cause inferior quality leaves. Commonly, whole plants of air-cured tobaccos are cut off just above the ground and hung in barns for several months until cured. Leaves of bright, flue-cured tobaccos are typically harvested individually as they ripen. These leaves are cured by heating them up slowly through yellowing, drying, and stem-drying steps. Piles of cured tobacco leaves are generally sold at auction in large, well-lighted warehouses.

Tobacco is believed to have originated in northwestern Argentina and adjacent Bolivia. Native peoples undoubtedly used it for centuries before Europeans colonized the Americas. Christopher Columbus was introduced to tobacco by the Arawaks on October 11, 1492, when he first visited the Caribbean islands. Tobacco smoking spread throughout Europe in the second half of the sixteenth century. Tobacco soon became the most important commercial crop in Colonial America, and the tobacco trade directly contributed to the success of the first permanent English settlement at Jamestown, Virginia.

Differences in cultural practices and diverse climatic and soil conditions produce several different types of tobacco that are used in various smoking and chewing products. The major types of tobacco are bright (flue-cured), light air-cured (burley), dark air-cured, fire-cured, oriental, cigar wrapper, and cigar filler. Burley and flue-cured tobaccos are the primary tobacco types

A Zimbabwean man working in a tobacco field. During harvest, tobacco is cut and placed on sticks and later taken to cure in drying barns.

used in the manufacture of cigarettes, and they account for most of the U.S. production. Over 90 percent of the tobacco grown in the United States is from North Carolina and Kentucky, but Maryland, South Carolina, Virginia, Georgia, Florida, Ohio, and Tennessee also produce substantial amounts of this crop.

Tobacco leaves are covered with trichomes (hairs) that have multicellular glands on their tips. These glandular trichomes produce a sticky resinous material that contains many of the flavor and aroma components. Tobacco also produces many internal, secondary components, including pyridine **alkaloids**. The most important alkaloid is nicotine, which acts as a stimulant to the user and is addictive. Nicotine is quite toxic, and products containing nicotine were used as early insecticides. The adverse health effects of smoking, including nicotine addiction and the increased risks of cancer, emphysema, and heart attack, are well documented.

alkaloids bitter secondary plant compounds, often used for defense

Tobacco has been extensively used as a model system in many basic scientific studies. Pioneering work in **quantitative** genetics, tissue culture techniques, plant **physiology**, and genetic engineering have utilized the unique characteristics of tobacco, which has been referred to as "the white rat of the plant world." SEE ALSO Alkaloids; Economic Importance of Plants; Poisonous Plants; Psychoactive Plants; Solanaceae.

D. Michael Jackson

quantitative numerical, especially as derived from measurement

physiology the biochemical processes carried out by an organism

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Torrey, John

American Botanist and Chemist
1796–1873

John Torrey.

John Torrey was one of the major botanists in the United States in the nineteenth century. As a youth he chose medicine as a career and in 1816 entered the College of Physicians and Surgeons in New York City. Before graduation he joined with his professors to become one of the founders of the Lyceum of Natural History of New York (now the New York Academy of Sciences). In 1818, he received his medical degree (M.D.). His first academic position was as an Assistant Surgeon and Professor of Chemistry and Mineralogy at West Point, New York. A few years later he was invited to return to his alma mater, and there he taught chemistry from 1827 to 1855. He also taught at Princeton from 1830 to 1854.

From 1820 until his death in 1873, Torrey was recognized as the major botanist of the innumerable plant collections by the many military expeditions sent by the U.S. government into the western lands of the Louisiana Purchase. Torrey assorted, arranged, named, diagnosed, and described new species by thousands. His life is in many ways a bibliography of early North American botanical exploration and discovery.

Torrey's first expedition papers analyzed plants collected during the Major Long Expedition in 1820 to the Platte River. Torrey's third paper on the tundra plants of the Rocky Mountains used the Natural System of classification, which had been recently introduced from Europe and had jarred many American traditionalists who still followed the Sexual System of classification as developed by Linnaeus. This shift was a major step forward in the American scientific community.

In 1832, Torrey met Asa Gray, a medical doctor. They commenced on a fruitful working relationship, and eventually Gray became one of America's greatest botanists, and, ultimately, Torrey's successor. "Torrey and Gray" were soon a kind of botanical statement as today "Watson and Crick" are.

In 1839, Torrey was named State Botanist of New York, and in 1843 he published the first *Flora of New York State.*

Retired from Columbia College in 1855, Torrey, then a trustee of the college, offered the administration his huge, well-known herbarium, asking to remain on campus as the curator. The college accepted and he lived on the campus until his death in 1873. Also a known mineralogist, Torrey was hired as the **assayer** of the New York Mint, which he continued until his death.

assayer one who performs chemical tests to determine the composition of a substance

In 1860, with the looming danger of the Civil War, Torrey volunteered to take temporarily the Smithsonian Herbarium to his New York Columbia Herbarium, where it was assumed to be safer. Torrey kept the materials for nine years, greatly increasing the number of **specimens** and working hard to improve the collection. The National Herbarium owes much to Torrey.

specimen object or organism under consideration

In 1867, a Manhattan botanical club, which was assisted by Torrey and which held its meetings in his herbarium, was renamed The Torrey Botanical Club (now Society). Today it is a national scientific society and holds its meetings in the New York Botanical Garden's Torrey Room. Torrey's herbarium is now the heart of the world-class Herbarium of the New York Botanical Garden. SEE ALSO Gray, Asa; Linnaeus, Carolus; Taxonomist; Taxonomy, History of.

Lawrence J. Crockett

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Transgenic Plants

Transgenic plants are produced when a gene from one plant is inserted into the **genome** of another. For the gene to work properly in the transgenic plant, it must be engineered to have a promoter before its start codon (to turn it on) and a terminator after its end (to turn it off). Generally the gene also needs some deoxyribonucleic acid (DNA) at either end that will allow it to be inserted into the host genome. The transfer DNA (tDNA) from the bacterial microbe *Agrobacterium* is used routinely for this purpose. Also required is an antibiotic resistance gene that will allow the transgenic plant cells to be recovered from a mixture with untransformed cells. In a typical project, the desired gene is engineered with the correct elements, placed in

genome the genetic material of an organism

vector carrier, usually a carrier who is not affected by the thing carried

a plasmid **vector**, and then inserted into *Agrobacterium* cells. *Agrobacterium* is then used to infect the plant cells with the plasmid vector. The tDNA allows the desired gene and the antibiotic resistance gene to be incorporated into the plant cell's genome. The transgenic cells are selected using the antibiotic in a tissue culture medium; only cells having antibiotic resistance as a result of transformation will survive on this medium. Finally, the transgenic cells are manipulated with the hormones in the tissue culture medium to regenerate whole transgenic plants. To be sure that the gene is inserted and is functioning, botanists will check for the presence of inserted DNA using a **Southern blot** and will confirm the presence of modified ribonucleic acid (RNA) with a **Northern blot**. Development of an expected phenotype in mature plants can also confirm the insertion. SEE ALSO BREEDING; GENETIC ENGINEER; GENETIC ENGINEERING; MOLECULAR PLANT GENETICS; TISSUE CULTURE.

Southern blot a technique for separating DNA fragments by electrophoresis, and then identifying a target fragment with a DNA probe

Northern Blot a technique for separating RNA molecules by electrophoresis, and then identifying a target fragment with a DNA probe

Ross Koning

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Translocation

Translocation is the process within plants that functions to deliver nutrients and other molecules over long distances throughout the organism. Translocation occurs within a series of cells known as the phloem pathway, or phloem transport system, with phloem being the principal food-conducting tissue in vascular plants. Nutrients are translocated in the phloem as **solutes** in a solution called phloem sap.

solute a substance dissolved in a solution

The predominant nutrients translocated are sugars, amino acids, and minerals, with sugar being the most concentrated solute in the phloem sap. Various cell types utilize these nutrients to support their requirements for life or store them for future use. Because translocation is responsible for the delivery of nutrients to developing seeds and fruits, this process is critical to the achievement of optimal crop yield. It also accounts for the ultimate nutritional composition of plant foods important to humans.

Various plant hormones, proteins, and nucleic acids are also moved throughout the plant via translocation. Hormones act as cues, or signals, to stimulate distant cells to alter their pattern of growth or to adjust various cellular machinery. Examples of such signaling events would be the conversion of vegetatively growing cells into reproductive tissues (i.e., flowers); an enhancement in the ability of root cells to absorb needed mineral **ions** from the soil (e.g., iron, zinc); or the synthesis of specific **compounds** in distant leaves to deter **pathogens** (e.g., insect feeding, fungal infections). Thus, the translocation of information molecules makes it possible for plants to correctly sense and respond to varying conditions or challenges in their environment.

ions charged particles

compound a substance formed from two or more elements

pathogen disease-causing organism

Pathway of Translocation

The movement of sugars and other molecules generally follows a path that originates in plant organs where sugars (the primary solute) are made and terminates in regions where these nutrients are utilized. The organs where the pathway begins are called source regions, or sources, and the ends of the pathway are referred to as sink regions, or sinks. The predominant organ for the manufacture of sugars is the leaf, which can take in carbon dioxide and light energy to produce sugars through the process of photosynthesis. These sugars can be used locally by the leaf or can be translocated to the rest of the plant. Leaves are generally considered the primary source regions, but it should be noted that only fully expanded, mature leaves can act as sources. Newly emerging leaves are unable to fully nourish themselves with their own sugar production, and thus they act as sink regions until they reach full maturity.

Other sink tissues include root systems, which cannot carry out the process of photosynthesis and must be fed by the leaves, and developing reproductive tissues, such as seeds and fruit, which store nutrients for future use. Additional storage organs that are translocation sinks and which are important human food crops include tubers (e.g., potatoes and yams) and tap roots (e.g., carrots and beets).

Plant structures that lie between terminal source and sink tissues, such as the stem of an herbaceous plant, the trunk and branches of a tree, or the petiole of a leaf, make up the translocation pathway. All of these structures contain numerous living cells that require nourishment and, thus, these pathway tissues can also function as sinks. In certain cases, however, they serve dual roles, because in some plants (e.g., cereals such as rice and wheat) the stems act as temporary storage organs for nutrients. At late stages in the plant's life cycle, these stems are converted to source regions that provide nutrients for the developing seeds. Various non-leafy green tissues that can conduct photosynthesis also can serve as sources; pea pods, for instance, can translocate sugars and other nutrients to the developing pea seeds.

Structure of Phloem Cells

The translocation of molecules via the phloem pathway is dependent on the functioning of specialized cells that are distributed in an organized manner throughout the plant. The cells that conduct nutrients over long distances are called sieve elements, of which there are two types: sieve cells, which are found in **gymnosperms** (e.g., conifers and cycads), and sieve-tube members, which are found in **angiosperms** (i.e., monocots and dicots). Sieve elements are narrow, elongated cells that are aligned in long columns that extend from source to sink regions within the plant. Sieve elements are living cells and thus possess a plasma membrane at their periphery, just inside the cell wall. However, they do not contain a nucleus at full maturity, and possess only a few cellular **organelles** (e.g., **mitochondria**, **endoplasmic reticulum**). The lack of a nucleus and most other cellular structures means that the cell interior is rather open. This serves to make sieve elements good conduits for long-distance solution flow.

gymnosperm a major group of plants that includes the conifers

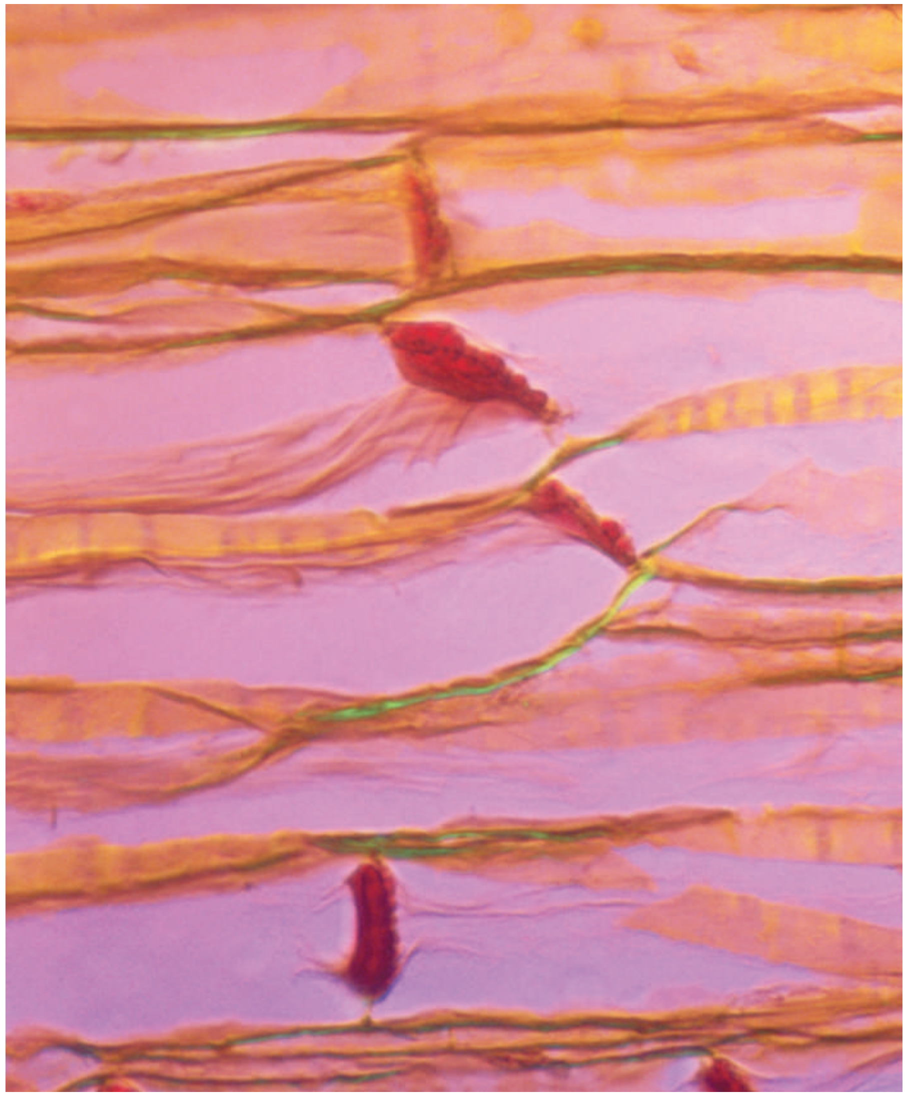
angiosperm a flowering plant

organelle a membrane-bound structure within a cell

mitochondria cell organelles that produce ATP to power cell reactions

endoplasmic reticulum membrane network inside a cell

The term *sieve* in the various names refers to the clusters of pores, or sieve areas, that perforate the common cell walls between adjoining sieve



Micrograph of phloem fibers and sieve tubes from the stem of a bryony plant (*Bryonia*), through which nutrients are transported.

elements and which interconnect these cells. The interconnection is possible because the plasma membrane of each sieve element is extended as a tube through each sieve pore. In sieve cells, the pores are narrow and the structure of the sieve areas is fairly uniform on all walls of the cell. Sieve cells are usually arranged with long, tapering, overlapping ends, and most of the sieve areas are concentrated on these overlapping regions. In sieve-tube members, narrow-pored sieve areas exist, but some walls also possess much larger pores. The areas with larger pores are called sieve plates, and are usually located on the end walls. These end walls tend to be less obliquely oriented than the ends of sieve cells, and in many species can be situated almost perpendicular to the long, side walls. Sieve-tube members are organized end-to-end in columns of cells called sieve tubes, thus forming a long tubular network throughout the plant. Their larger end-wall pores means that the phloem sap can be more readily translocated over long distances.

The cell walls of sieve elements are considered primary walls, as they are composed chiefly of cellulose. The pores of the sieve areas and sieve plates are additionally lined with a substance called callose, which is a **polysaccharide** consisting of glucose units. The role of callose in the vicinity of

polysaccharide a linked chain of many sugar molecules pores is to act as a sealing agent in the case of injury to the phloem pathway. When a plant structure is damaged by mechanical stress, such as wind, or by biological attack, such as feeding by an insect, the plant could lose nutrients if these were to "bleed" from the cut end of the sieve elements. This usually does not happen, because following injury callose is rapidly deposited within the wall region of sieve pores. This deposition constricts the interconnecting tube of plasma membrane and thereby blocks the pore. With time, the plant can generate new sieve elements around the cut area to reestablish translocation within that column of phloem cells.

As mentioned earlier, sieve elements do not contain a nucleus in their mature state, yet in some species sieve elements are known to live for decades. How is this possible? Sieve elements are always found to be associated with specialized accessory cells that contain all the components commonly found in living plant cells, including a nucleus. For sieve-tube members, these specialized cells are called companion cells, and the specialized association is referred to as the sieve element-companion cell complex. Companion cells are very densely filled with organelles, and thus they are not structurally suited for the long-distance translocation of nutrients. Functionally, however, companion cells are extremely important, as they are responsible for the coordinated movement of molecules into and out of the sieve-tube members. These molecules include not only substances translocated throughout the plant, but also proteins and nucleic acids that are needed to maintain the life and functions of the sieve-tube member. The movement of these molecules occurs through elaborate channels called plasmodesmata that interconnect companion cells and sieve-tube members. Less specialized plasmodesmata also exist between certain other cell types. Although very important, the movement of molecules through plasmodesmata is poorly understood, and scientists are currently focusing much attention on this area of plant biology.

Accessory cells are also found associated with the sieve cells of gymnosperms, where they are called **albuminous** cells. The albuminous cells are structurally comparable to and perform a role similar to that of companion cells.

albuminous gelatinous, or composed of the protein albumin

Loading and Unloading of Sugars and the Pressure-Flow Mechanism

With the presence of a continuous, membrane-bound pathway, phloem sap can flow from source to sink regions within the plant. But how do the components of the phloem sap get in to or out of the pathway, and what is the mechanism, or driving force, that moves the solution? As noted earlier, the predominant solute in phloem sap is sugar, and in many species the translocated sugar is sucrose. For these species, sucrose is manufactured primarily in the photosynthetic mesophyll cells of the leaf, from where it must be transported to the minor veins of the phloem system. Sucrose can move to the minor veins using an **intracellular** pathway, referred to as symplastic movement, or it can diffuse through a path along the cell walls, a process known as apoplastic movement. In either case, sucrose is eventually pumped into sieve elements through an active, energy-requiring process called phloem loading. The amino acids and mineral ions found in phloem sap also are said to be "phloem loaded."

intracellular remaining inside cells

What phloem loading accomplishes is to create a very high concentration of solutes within the interior of the sieve elements in a source region. Because the sieve element interior is surrounded by a largely non-permeable plasma membrane, it is able to retain these solutes within the cell. On the other hand, the plasma membrane also contains special channels that make it highly permeable to water molecules and water molecules enter by **osmosis.** This is critical because the movement of water into sieve elements increases the hydrostatic pressure (i.e., the water pressure) of phloem sap within these cells. The end result is that the interior of the sieve element becomes pressurized with respect to other cells of the source region.

osmosis the movement of water across a membrane to a region of high solute concentration

At the sink end of the pathway, an opposite chain of events is occurring. Sugars and other solutes are moved out of the sieve elements through a process called phloem unloading, as these solutes are used by other cell types for growth, metabolism, or storage. In response to this release of solutes water molecules move out of the sieve element, and the result is a localized decrease in the sieve element hydrostatic pressure. The lowered pressure within the sieve elements of the sink region in conjunction with the higher pressure within the sieve elements of the source region creates a **gradient** of pressure along the length of the interconnected phloem pathway. Because of this pressure gradient, a bulk flow of phloem sap occurs from high to low pressure, or from source to sink tissues. The pressure gradient remains in place, even as flow proceeds, as long as solutes are continuously loaded into and unloaded from the pathway. This translocation process is known as the pressure-flow mechanism.

gradient difference in concentration between two places

It should be noted that the larger the gradient in pressure between two points in the pathway, the greater the potential for translocation of phloem sap. Thus, actively photosynthetic tissues have the ability to load more sugars into the pathway, creating higher localized sieve element pressures in these regions. Similarly, an actively growing sink tissue, which is consuming/removing large quantities of sugars and other solutes from the pathway, will create lower localized sieve element pressures in this region, which will help sustain translocation flow to the sink.

Ways to Determine the Chemical Nature of Phloem Sap and the Rate of Translocation

Scientists have been interested in studying the composition of phloem sap for many years because of its importance to plant growth and development. Unfortunately, access to pure phloem sap is difficult for a number of reasons: sieve elements are very narrow cells (approximately 10^{-8} meters in diameter), they are embedded within other tissues of the plant, and most plants have a sealing mechanism that prevents the loss of phloem sap upon cutting. Certain techniques do exist, however, that get around these problems. One approach involves the use of aphids, which are insects that feed selectively upon the contents of sieve elements but do not induce a sealing reaction. Scientists allow an aphid to insert its stylet, a long tube-shaped mouth part, into the side of a sieve element within a stem or leaf. The insect is then sacrificed and removed, with its stylet still inserted in the plant tissue, either by using a razor blade or a laser burst. Because the phloem sap is pressurized, phloem sap will flow out the cut end of the stylet for a short period of time and it can be collected for analysis. Standard analytical chemistry techniques are then used to determine carbohydrate and mineral composition of the phloem sap, or more modern techniques of protein chemistry and molecular biology are used to quantify and characterize the protein and nucleic acid composition of the collected solution.

The rate of translocation in different plants, especially in response to various environmental conditions, is also of interest to scientists who study phloem function. Because sugars are the predominant component of the phloem sap, researchers have used radioactively labeled sugars to monitor and quantify phloem translocation. A source leaf, for instance, can be exposed to radioactive carbon dioxide within a sealed glass chamber, allowing it to convert the carbon dioxide to radioactive sugars via the process of photosynthesis. These sugars are phloem loaded and can be monitored as they move throughout the plant using external radiation detectors, or sink regions can be harvested and analyzed for radioactivity following some period of translocation. In either case, rates of translocation can be quantified, and the effect of various physical or biological factors on translocation rate can be determined. These types of studies help scientists determine ways to improve plants, both in terms of yield and nutritional quality. SEE ALSO LEAVES; PHOTOSYNTHESIS, CARBON FIXATION AND; STEMS; VASCULAR TISSUES.

Michael A. Grusak

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Transpiration *See Water Movement.*

Tree Architecture

Most people are familiar with the shoot systems of trees but few people know much about their root systems; fewer still know much about how the architecture of trees helps them stand up against the major natural force threatening to topple them: the wind.

Trees typically have a single woody trunk that projects many meters vertically from the ground. Only toward the top of the tree does repeated branching form ever-narrower branches and twigs, which together make up the compact crown where most of the leaves are held.

It is a commonly held fallacy that the root systems of trees belowground are mirror images of the shoot systems aboveground. The roots do branch, and they extend radially about the same distance from the trunk as the crown, but here the resemblance ends. There is no belowground equivalent of the trunk because the central tap roots of most trees grow very slowly as the tree matures. Instead the system is dominated by several woody **lateral** roots, which grow horizontally away from the tap root, before branching into smaller, more

lateral to the side of

distal further away from

fibrous, **distal** roots. The vast majority of the root system therefore grows within a meter of the soil surface where the distal roots obtain resources from the nutrient-rich topsoil. Only the tap root and a few sinker roots that grow vertically down from the woody laterals penetrate down to the subsoil.

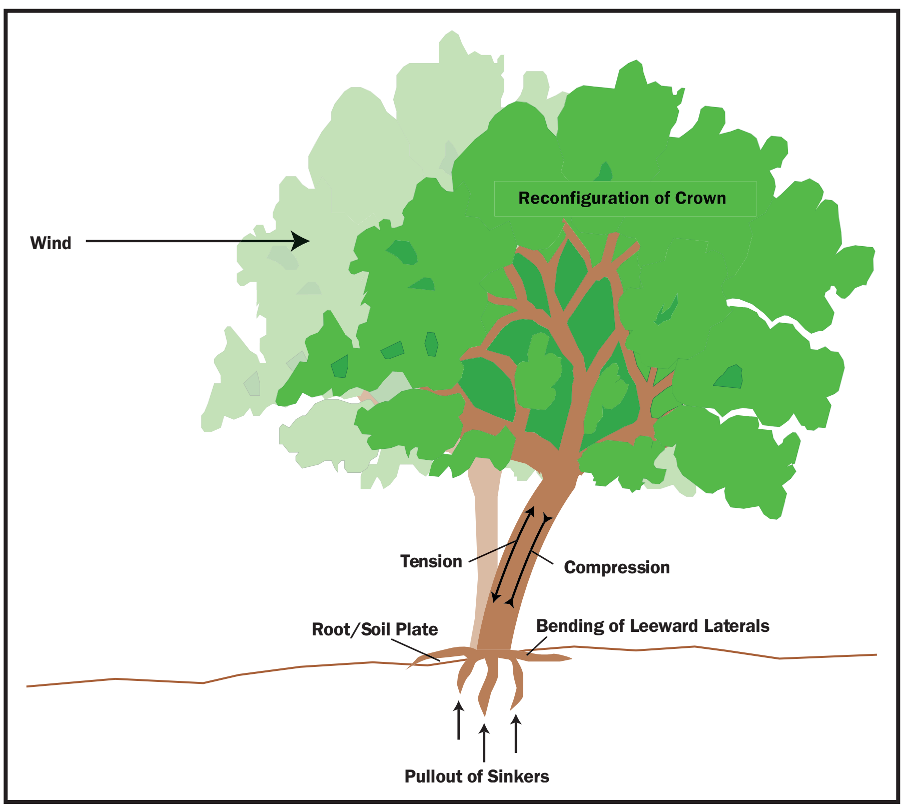
Mechanics of Wood

tensile forces forces causing tension, or pulling apart; the opposite of compression

The form of the woody parts of trees, both above and belowground, is strongly influenced by their mechanical function of raising the leaves above other plants, and so outcompeting them for the light. The material of which trees are made—wood—is apparently well designed to withstand the overturning forces caused both by the weight of the tree itself and, more importantly, the wind. Whenever the crown of a tree is blown by the wind the branches and trunk are both bent. This results in longitudinal **tensile forces** being set up along the windward side, and longitudinal compressive forces being set up on the leeward side. Both forces are efficiently resisted by the walls of the wood cells, which are arranged longitudinally like densely packed drinking straws.

Mechanics of the Shoot System

The aboveground architecture also plays a key part in preventing toppling. The single trunk is better at holding up the crown against strong wind forces than many separate trunks with the same total diameter. This is because the rigidity of a beam is proportional to the fourth power of its radius, whereas its weight is only proportional to the square of the radius. Hence a single trunk will be twice as stiff as two trunks with the same combined mass, and will be able to hold up the crown even in high winds. The



Mechanical changes that occur when a tree is blown by the wind. Above ground the trunk is bent, putting the leeward side into compression and the windward side into tension, while the crown reconfigures. Meanwhile, below ground the leeward laterals are bent and a root/soil plate is levered out of the ground, pulling up the sinker roots.

much thinner branches and twigs from which the crown is formed, meanwhile, are much better able to bend away from the wind. This reconfiguration helps to streamline the crown and reduce the forces it experiences. This streamlining can be improved by two other mechanisms. First, the leaves themselves reconfigure, folding up together with others along the same branches to reduce drag, while the lobed and pinnate leaves of some broad-leaved trees can each individually roll up into a streamlined tube. Second, in exposed areas wind forces reduce growth on the windward side of the crown and bend branches permanently to leeward. This produces a crown with a permanently streamlined "flagged" shape that presents less drag to the prevailing wind.

Mechanics of the Root System

Even with all of these drag-reducing mechanisms, overturning forces are still transmitted to the trunk and hence to the root system. Fortunately this is also well designed to resist failure. The extensive woody laterals prevent the leeward side of the root system from being pushed into the ground. Instead, the likely mode of failure is for a windward root/soil plate to be levered out of the ground. This movement is resisted strongly by the weight of the soil plate and the resistance of the leeward roots to bending. But the greatest component of anchorage is provided by the sinker and tap roots, which must be pulled out of the ground; their vertical orientation, reminiscent of that of tent pegs, is ideal to resist this movement. The result is that a fairly small woody root system can effectively anchor a large tree.

Growth Responses of Trees

The genetically determined architecture of trees is therefore ideally suited to resist mechanical failure. Their mechanical efficiency is further improved by a growth response called thigmomorphogenesis. The higher the mechanical stresses imposed on trees by the wind, the more wood they lay down to strengthen their structure; consequently trees growing in exposed areas develop shorter but thicker trunks, branches, and roots. In contrast, if a tree grows in a sheltered wood it will grow taller and thinner, improving its chances of reaching the light. A further refinement, which was first suggested by Claus Mattheck, is that the growth response is locally controlled. Wood is laid down fastest in the areas subject to the highest stress and these areas are consequently strengthened. This response ensures that there are no weak areas in the tree, and it also improves the mechanical design. It automatically ensures that branches are joined to the trunk with smooth fairings and that the vulnerable sides of wounds heal fastest. Research also suggests that it might be responsible for the growth of one of the most bizarre features of rain forest trees: the platelike buttresses that join the superficial lateral roots to the trunk like angle brackets.

The combination of efficient material design, good above and below-ground architecture, and adaptive growth responses have ensured that trees can survive even in the face of terrible gales. Moreover, they are the largest and most spectacular of all biological structures. Giant redwoods can grow well over 100 meters tall, weigh over 1,000 tons, and live for over 1,000 years. SEE ALSO Anatomy of Plants; Roots; Trees.

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Trees

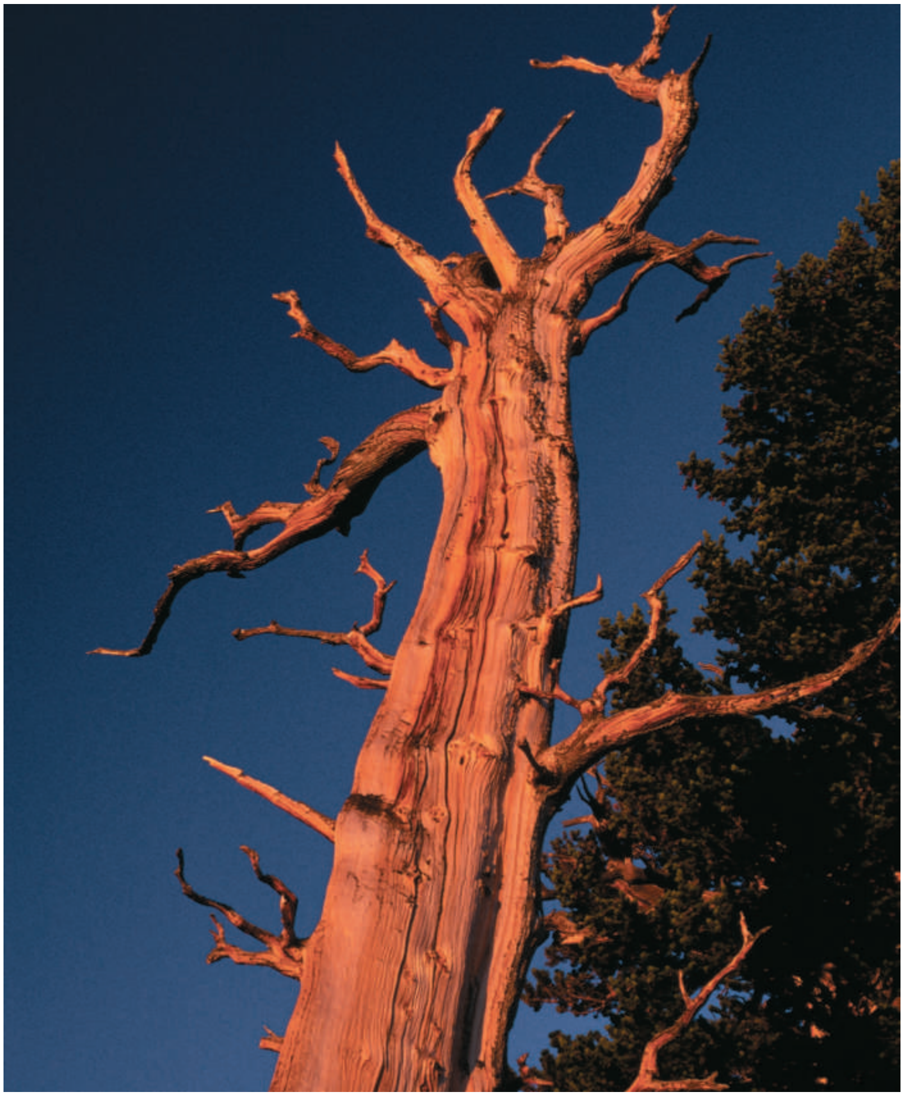
Trees are plants with an erect perennial stem at least 4 meters (13 feet) tall, a diameter measured at breast height (1.3 meters or 4.5 feet) of at least 7.5 centimeters (3 inches), and a distinct crown of leaves or leafy branches. This definition is widely used by foresters and forest ecologists to divide woody plants into trees, shrubs (smaller plants, often with clustered stems), and vines (plants not self-supporting and usually without a distinct crown). However, plant species are not constrained to fit definitions, thus plants of the same species may grow as trees in some areas and as shrubs in others, especially at the edge of the species' range where growing conditions are harsh. Thus lodgepole pine, valued by Native Americans for its tall, straight "lodge poles," becomes a sprawling shrub near timberline in the Rocky Mountains and on sandy beach dunes of the Pacific Coast.

Trees are usually woody; that is, their stems are composed largely of densely packed, elongated, thick-walled cells (secondary wood) produced by a cylindrical growing center, the vascular cambium, that surrounds the stem underneath the bark. Typically the secondary cambium adds new wood throughout the life of the tree, gradually increasing the trunk diameter as the crown grows larger and taller. Notable exceptions occur in tree ferns, cycads, palms, and a few other plants that reach tree dimensions while producing little or no secondary wood. In these plants neither trunk diameter nor crown size increases much with age once the single apex of large compound leaves reaches mature size. However, mechanical support by the stem is often aided by an encircling band of tightly packed roots (e.g., tree ferns) or persistent leaf bases (e.g., cycads and palms).

vascular plants plants with specialized transport cells; plants other than bryophytes

Trees are regularly associated with certain plant groups such as the oak (oak, beech, chestnut) and pine (pine, spruce, fir, hemlock, etc.) families; however, most families of **vascular plants** contain some tree species. Residents of temperate climates are often surprised to find that tomatoes, violets, shrubby sumacs, and even grasses have close tropical relatives that are trees. Today's diminutive club mosses, spike mosses, and quillworts (order Lycopodiales) and horsetails (order Equisetales) are the remaining relatives of huge scale-trees (Lepidodendrales) and giant horsetails (Calamitales) that dominated swampy forests in the Carboniferous (coal-forming) period of Earth's history three hundred million years ago.

Trees are the giants of the plant world. Among the tallest ever measured was a Douglas-fir (*Pseudotsuga menziesii*) in Washington that measured 117 meters (385 feet) tall. California claims the tallest living tree, a coast redwood (*Sequoia sempervirens*) 112.6 meters tall, but competing for this distinction are trees of *Eucalyptus* in Australia, which are perhaps a few meters



A bristlecone pine tree on Mount Evans, Colorado. Bristlecone pines are the oldest trees in North America and perhaps the world.

taller. In total weight or **biomass**, probably no other species has ever produced larger trees than the Big Tree redwoods (*Sequoiadendron giganteum*) of the California Sierra Nevada Mountains. These colossal giants (to 88 meters) maintain their basal diameter of 5 to 10 meters with little taper to the base of their crown over 40 meters high.

biomass the total dry weight of an organism or group of organisms

Big Tree redwoods are also among the oldest known trees, reaching ages of more than three thousand years. However, the oldest trees in North America and perhaps in the world are quite modest in size (10 × .6 meters). These belong to a species called bristlecone pine (*Pinus aristata*). The oldest bristlecone pines (more than forty-six hundred years) grow in dry rocky soils near timberline in southern California where the harsh growing season is very short and annual growth in trunk diameter is often less than 0.2 millimeters. Age estimates of bristlecone pines are obtained by counting annual growth rings in studies collectively termed dendrochronology. The science of dendrochronology uses tree-ring information to reconstruct long records of climatic history and to date prehistoric wooden structures.

Trees and Forest Types

Trees greatly modify the habitat in which they live, by their shade and by their litter of fallen leaves. Typically light-loving tree species occupy the highest section of the forest, the overstory or canopy, with shade-tolerant species below. Species inhabiting these forest layers differ according to geographic and **topographic** location and associated climate and soils. Forest composition may also differ with age, and to some degree, by chance, that is, which species managed to get its seeds to the area first or survived the longest. Despite these causes of forest differences, it is possible to recognize common associations of particular plant species with particular habitats. For example, ecologists and foresters usefully refer to Oak–Hickory forests as tending to occur on dry upland areas in the east central United States, with Beech–Maple forests tending to occur on more moist north-facing slopes. Many such forest communities are recognized across the country and are often named for their two most common overstory trees.

topographic related to the shape or contours of the land

Perhaps the greatest contrast between forest types in temperate regions is between deciduous broad-leaved and evergreen coniferous forests. In deciduous forests light penetrating to the forest floor in early spring supports a diverse array of spring wildflowers and ferns whereas the perennially dark floor of a dense coniferous forest supports many fewer species.

Tree Uses

It is hard to overestimate the importance of trees in their many uses for lumber, landscaping, shade, ornamental plantings, and windbreaks. In all of these uses diversity among trees is important. Wood types differ in strength, weight, hardness, color, figure, and other characteristics. Even taste can be important where cooking utensils or food storage is the use. Usually fast-growing trees such as cottonwood produce light, soft wood relative to that produced by slow-growing trees such as oaks and hickories. Conifers (often called softwoods) are preferred for construction lumber where ease of cutting, carrying, and nailing is important. The heavier, stronger, tougher wood of flowering trees (hardwoods) is preferred for railroad ties, strong crates, hardwood floors, tool handles, and sports equipment. Because of their attractive color and grain, hardwoods are also favored for fine furniture, cabinetry, and wall panels. All species and all sizes of trees are used for pulp and wood flakes for paper products and synthetic lumber.

Tree Diversity

To meet the need for diverse wood products, naturally diverse forests must be maintained. More than 600 species of native trees occur in North America north of Mexico, but much greater diversity occurs in tropical forests. A single hectare (2.5 acres) of Amazon forest may contain more than 200 different species whereas the most diverse U.S. forests contain about 20 species per hectare. In addition to variety in wood products, tree diversity aids forests in resisting diseases and pests and promotes wildlife diversity through the variety of foods, dens, and perching and nesting sites they maintain. Tropical rain forests' tree canopies support an array of epiphytic mosses, ferns, and flowering plants and hundreds of insect and larger animal species that scientists are just beginning to explore.

Tree Identification

Tree identification is necessary for forest and tree management and a rewarding hobby enjoyed by many nonprofessionals. Books aiding identification and describing trees, tree uses, and tree care are available for nearly all areas, ranging in coverage from local regions to entire countries and continents. Leaf size, shape, and arrangement on the stem are often sufficient to identify a tree, but twigs, bark, fruits, cones, and sometimes flowers may be required. Winter identification of deciduous trees by twigs and bark presents a special challenge, but one that can be mastered by the dedicated student. SEE ALSO Chestnut Blight; Coniferous Forests; Conifers; Deciduous Forests; Dendrochronology; Dutch Elm Disease; Forester; Forestry; Gymnosperms; Palms; Rain Forest Canopy; Rain Forests; Record-Holding Plants; Sequoia; Tree Architecture; Wood Anatomy; Wood Products.

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Trichomes

Trichomes are single or multicellular outgrowths of the plant epidermis and collectively constitute the pubescence (hairiness) of the plant surface. These epidermal hairs in many plant species are specialized for defense against attack by insects and mites. The mode of defense used by trichomes is determined by whether they are nonsecretory or glandular, as well as their density, length, shape, and degree of erectness. When present on the plant surface at high densities, **nonsecretory** trichomes create a physical barrier to insect feeding on the underlying surface or internal tissues. Barrier defense is an important element of resistance to leafhoppers in cultivated crop plants such as alfalfa (*Medicago*), cotton (*Gossypium*), and soybean (*Glycine*). Although not defensive, similar but downward-pointing trichomes in the upright tube of the carnivorous pitcher plant (*Sarracenia*) create a "lobster pot" effect preventing the escape of prey. Beans (*Phaseolus*) have evolved fish-hook-shaped trichomes that help to anchor their climbing vines but the hooked feature is also defensive because leafhopper and aphid pests are impaled and captured by these hairs. The most elegant specializations of plant hairs for defense are glandular trichomes, which secrete adhesive materials that physically entrap and immobilize insects and mites or which contain toxic or deterrent substances. Trichomes of this type are common in the nightshade family (Solanaceae) and plant breeders have created new varieties of potatoes (*Solanum*) and tomatoes (*Lycopersicon*) that resist insect pests because of glandular hairs on their leaves and stems. Other crop plants in

nonsecretory not involved in secretion, or release of materials

A praying mantis perched atop a pitcher plant. Trichomes in the upright tube of the carnivorous pitcher plant (*Sarracenia*) create a "lobster pot" effect, preventing prey from escaping.

which glandular trichomes are being used to breed for pest resistance include alfalfa, strawberry (*Fragaria*), sunflower (*Helianthus*), and tobacco (*Nicotiana*). SEE ALSO Carnivorous Plants; Defenses, Chemical; Defenses, Physical; Halophytes; Leaves.

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Tropisms and Nastic Movements

Unlike animals, plants cannot move to more favorable locations. Instead, plants survive by adjusting their growth to their local environment. A major way this is done is by sensing the directions of environmental signals such as light and gravity. This sensory information is then used to orient the direction of growth toward or away from a stimulus in a process called a tropism. By these mechanisms, shoots grow up from the ground and into the light. This enhances photosynthesis and biomass by increasing the amount of sunlight absorbed by chlorophyll. The raised stature of the plant also promotes pollination and seed dispersal, and increases plant competitiveness.

Tropisms are different from nastic movements. Like tropisms, these plant movements are influenced by environmental cues. But the direction of a nastic movement is independent of where the signal comes from, and most such movements are temporary. Nastic movements are more specialized in function and distribution than tropisms. For example, some **insectivorous** plants capture prey by moving trap organs together.

insectivorous insect-eating

Tropisms should not be confused with tactic movements found in many microorganisms, such as a unicellular green alga that moves toward the light (phototaxis). Because plants are not **motile**, only part of their body grows in the direction of a stimulus.

motile capable of movement

Tropisms

In tropisms, the growth of a plant organ is oriented by an environmental signal. Usually the organ grows toward or away from the stimulus. The former is considered to be a positive tropism, whereas growth away from a stimulus is a negative tropism. Houseplants on a windowsill grow toward the light by positive phototropism. Stems that emerge from seeds buried in the soil grow upward away from gravity by negative gravitropism. Tropisms can also occur at other angles with respect to a stimulus. Modified stems, called rhizomes, grow along the surface of the soil at right angles to gravity, such as in iris plants. Phototropism and gravitropism are by far the most important and widespread of tropisms in plants. In some plants and organs, other physical stimuli, including touch, temperature, and water, can orient growth as well.

Tropisms allow plants to adjust the direction of growth when their environment changes. For example, when a seedling is turned on its side, the root grows gradually downward creating a curvature, an example of positive gravitropism. This occurs in the growing region of the root, a region located close to the root tip. Once the root tip points downward again, the root stops curving and the subsequent growth is straight. After a region responds to a stimulus its orientation is usually permanent. For example, the curvature remains for the life of the root.

In most cases, only the growing regions of the plant are capable of tropisms. There are many such regions in a plant. The tips of stems and roots contain meristems, regions where new growth occurs. Cell divisions in meristems contribute to the elongation of stems and roots, and form new stem branches. Each stem branch is capable of phototropism and gravitropism. Their collective responses help determine the overall shape of the shoot.

By definition, a tropism involves a stimulus that contains some directional information. With gravity, both the direction and strength of the stimulus are uniform. In contrast, the direction of illumination constantly changes, and even heavily shaded plants receive at least some light from all directions. Two conditions must be fulfilled for a tropism to occur in such situations. First, the stimulus must exist in a **gradient** with respect to the plant. Thus the light is brighter on one side of a shoot, or there is more

gradient difference in concentration between two places

Form corn seedlings sprouting in a petri dish. When seedlings are turned on their sides, their roots grow gradually downward and create a curvature, an example of positive gravitropism.

water on one side of a root. Second, this gradient must last long enough to influence growth. Because a tropism results in a permanent change in position, it would be wasteful for plants to respond to short-lived changes in the environment.

All tropisms include two major stages, sensing and the growth response. The direction of the signal must first be sensed. Sensing means that physical information in the environment is somehow converted into biological information in the plant. This biological information is then interpreted in the growing zone resulting in guided growth. When a root is placed on its side, it curves downward because the upper side of the root grows faster than the lower side. The end result is that directional information about a physical signal is translated into different rates of elongation to produce directional growth.

Much of the research done on tropisms tries to understand how sensing and differential growth take place. Although scientific understanding of these processes is still incomplete, there have been some important advances, especially since the late 1980s and the development of genetic analytical techniques.

Phototropism. Phototropism is one of the most significant tropisms for plant survival because it positions shoots where more light for photosynthesis is available. It is especially important during seedling emergence and when plants are shaded unequally.

Sensing. One of the first important studies of plant tropisms was of phototropism by Charles Darwin and his son Francis over a century ago. They tried to determine where light is sensed in the coleoptile, which is a leaflike sheath that covers and protects emerging grass seedlings. As in current phototropism experiments, they exposed the seedling to light from just one side. Coleoptiles whose tips were cut off or were kept dark by a hood did not grow toward the light. However, if the tips were covered by transparent material or if the base of the coleoptile was kept dark, then the coleoptiles grew towards the light. They concluded that the tip of the coleoptile is largely responsible for sensing the light during phototropism.

However, coleoptiles are an unusual organ found only in grasses. In stems, the most common phototropic organ, the site of sensing seems to be more spread out. Even stems whose tips were covered and darkened were capable of bending toward a light from the side.

One reason why the precise site of stem sensing is unclear is that the pigment responsible was unknown for many years. Light acts when it is absorbed by a pigment-containing molecule. For many years, scientists knew that blue light is the most effective color in causing phototropism. Green or red light were either ineffective or caused only slight bending. Scientists tried to find pigments isolated from plants that especially absorbed blue light, but that did not absorb green or red light. Two types of **pigments** had these characteristics, **carotenoids** and flavin-containing molecules. But this information was not enough to identify the particular molecule responsible. One reason for this is that there are many types of blue-light responses in plants in addition to phototropism.

pigments colored molecules

carotenoid a colored molecule made by plants

As in so many other areas in plant biology, recent studies using the model plant *Arabidopsis* resulted in rapid progress in phototropism. A mutant was isolated, non-phototropic 1 (nph1), which fails to grow towards blue light. The affected gene was found to code for a protein that binds to a flavin molecule. It is likely that the combination of this protein and a flavin pigment molecule is responsible for phototropism. The identification of this molecule provides an important foundation for future research.

Growth response. The Darwins showed that light sensing takes place in the tip of the oat coleoptile and that phototropic curvature occurs several millimeters below the tip. This separation suggests that there is communication between these two regions. Subsequent studies provided evidence for a chemical signal that moves from the tip to the base. This signal can move through the water in a gelatin block. In 1926 Fritz Went isolated this chemical and named it "auxin." In the 1930s, auxin was identified as the molecule indoleacetic acid (IAA). IAA was found to cause many effects in plants in addition to phototropism, and auxin is now recognized as a major plant hormone.

Auxin moves from the tip of a coleoptile towards the base. Under some circumstances, auxin can also move from one side of the organ to the other. A major effect of auxin is to stimulate stem elongation. When coleoptiles are illuminated, auxin moves from the lighted side to the dark side. This **lateral** movement occurs in or close to the tip of the coleoptile. The auxin then moves down to the growing part of the coleoptile. The presence of more auxin in the dark side causes that side to grow more than the illuminated side. This causes the coleoptile to curve towards the light. Similar events appear to occur in stems.

lateral away from the center

In summary, a light gradient is sensed by a flavo-protein pigment molecule. Light absorption somehow increases the amount of auxin on the dark side of the growing zone, which causes more growth on that side and curvature towards the light.

Phototropism and solar tracking. It is often easy to detect the effects of phototropism in nature. It can be seen when stems emerge from the ground, or when part of a plant is more shaded than another. Unequal shading can be produced by other plants, or by objects such as rocks, logs, and walls. In contrast, phototropism is rare in a mature plant that is growing in an open, sunny area. This is because the movement of the sun during the day and the season is too fast and variable to allow phototropism to develop.

However, in a few plants, the leaves do follow the sun during the day. The leaf stalk twists during the day so that the leaf blade keeps facing the sun. The result is an increase in photosynthesis. This phenomenon, known as solar tracking, is not a tropism because there is no permanent change in the direction of growth.

Gravitropism. Gravitropism helps plants flourish. The importance of gravitropism can be illustrated by the maize (corn) plant. The upward growth of the stem raises the leaves up. The base of each leaf is also oriented by gravitropism at a set angle. The result is that the leaves become located in the position that exposes them to the most light. The raised stature also allows the plant to compete with other plants for sunlight. The upward growth also positions the pollen-producing flowers at the top of the plant where it can be carried by the wind to pollinate the female flowers (the silks). Some roots grow straight down, but others only do so after the roots reach a certain length. The result is well-branched root system that is distributed throughout the soil in a coordinated manner. This positions the roots near new supplies of water and minerals. It also anchors the plant to prevent it from falling over. Gravitropism helps optimize the growth of all of parts of this maize plant.

Gravitropism has a profound effect on the shape and form of many plants in addition to maize. Its influence is obvious in plants with pronounced vertical stems such as pine trees. Careful observation will also reveal subtler effects of gravitropism in other plants. Many stems and branches that are not vertical still grow at a more or less set angle with respect to gravity. This angle may vary with age and lengthwise position, but if a regularity is observed, it is likely to represent gravitropism. Indeed, gravitropism probably shapes plant life more than any other tropism.

organelle a membrane-bound structure within a cell

chloroplast the photosynthetic organelle of plants and algae

Sensing. How might a plant sense the direction of gravity? Unlike light, gravity cannot be absorbed by a molecule. Instead it must act on some dense structure. A century ago, German scientist Gottlieb Haberlandt observed that gravitropic organs contain heavy starch-filled bodies that fall or sediment. These bodies are **organelles** called amyloplasts. They are a type of plastid, special organelles in plants that include **chloroplasts**. Starch is dense and thus amyloplasts are heavy. Amyloplasts are found in many different locations in plants. But they only sediment in specific locations, such as the rootcap at the tip of roots and the starch sheath in the growing zone of stems. Haberlandt proposed that the falling of amyloplasts triggers gravity sensing. Most data support Haberlandt's hypothesis. For example, all natural, gravitropic organs have sedimented amyloplasts. And stems of the *Arabidopsis* "scarecrow" mutant are not gravitropic probably because they lack both a starch sheath and sedimented amyloplasts.

But this hypothesis was challenged when several mutants were found that do not have any starch but that are still gravitropic. This shows that starch is not necessary for gravitropism. However, the gravitropism in these mutants is defective, and they are much less sensitive to gravity than normal plants. This suggests that starch normally plays a role. But how might starchless mutants sense gravity, albeit poorly? Even these mutants still have plastids. Perhaps the starchless plastids can still function mechanically in sensing, but more poorly because they are lighter. When starch is present, there is more mass and probably a stronger signal as well.

Growth response. The mechanisms of gravitropic curvature are thought to be similar to that of phototropic curvature. The lower side of a stem probably has more auxin than the upper side, resulting in faster growth on the lower side and upward curvature. In roots it is thought that a higher concentration of auxin inhibits rather than stimulates growth. Thus more auxin on the lower side would cause it to grow more slowly than the upper side, causing downward curvature. The involvement of auxin in gravitropism is strongly supported by the isolation of two different types of mutants in *Arabidopsis* whose roots are not gravitropic. In each case, the mutated gene was found to disrupt the function of proteins that are probably necessary for auxin transport.

Thigmotropism. Thigmotropic organs grow around an object that touches them. When a tendril on a pea leaf or the stem of a vine come in contact with an object, they cling to and wrap around it. Thigmotropic shoots avoid the expense of making their own support tissue. Instead, they depend on an object to help them climb and position their leaves into the light. Vines and tendrils typically locate a support through slow sweeping movements. These movements stop when contact is made with a support. Pea tendrils respond to contact in two stages. They first quickly coil around the object through changes in water pressure of the cells. The outer part of the tendril then grows much faster than the inner part. The mechanism of sensing is not known. But in some plants, contact induces a wave of electrical signals down the organ. And thigmotropic organs might contain specialized stretch receptors such as membrane proteins that allow **ions** to pass through them when they are mechanically stimulated. Roots are also capable of thigmotropism. This probably helps them grow around hard objects in the soil.

ions charged particles

Roots also exhibit hydrotropism and electropism, which are growth responses to gradients in water and voltage. Electropism probably does not operate in nature, but scientists have used it to study root growth, including on NASA's Space Shuttle. Hydrotropism is obviously adaptive to guide root growth towards water. But root growth is much more affected by gravitropism, and in some plants by negative phototropism, than by hydrotropism.

Nastic Movements

In tropisms the direction of the stimulus controls the orientation of growth, and the effect is more or less permanent. In nastic movements, the direction of the response results from the structure of the organ, and it is only the quality, rather than the direction, of the stimulus that triggers a response. Most nastic movements are reversible. Unlike tropisms, which are found in virtually all plants, nastic movements are mostly found in specialized plants and organs.

Nyctinasty and Photonasty. The quality and intensity of light can cause organ movements. In many plants, such as legumes (members of the bean

An open sensitive plant (*Mimosa*).

family), the leaves move downward or fold at the end of the day. In other plants such as tulips, it is the flowers that close as night approaches. These nyctinastic or "sleep" movements are triggered by changes in the color and intensity of sunlight at the end of the day. The organs open up again around dawn.

The "light-off" and "light-on" signals interact with internal rhythms in plants. The light signals are used to set the internal clock, but are not actually required for movement. Once the rhythm is set, the leaves open and close in the dark at the correct times for several days.

Sleep movements help protect leaves and flowers from damage at night, but many plants survive quite well without such movements. Some plants that grow in the shade show photonastic movements. The leaves of wood sorrel (*Oxalis*) fold up during the day if the sun gets too strong This protects the pigments in the leaves from sun-induced damage. Leaves can also curve downwards in response to other signals (epinasty) such as when roots are flooded. Although light and dark can cause nastic movements in plants, there are no gravinastic movements. Gravity is not useful as a signal of changes in the environment because it is constant in presence and extent.

Thigmonasty and Seismonasty. Organ movements can also be induced by touch (thigmonasty) or shaking (seismonasty). These two types of nastic movements are related but distinct. The leaves of the sensitive plant, mimosa, fold up when they are touched by a falling object or an animal. They also close when they are shaken such as by the wind. This closing may reduce evaporation from the leaf in a strong wind, or discourage an animal from eating it.

In contrast, the closing of the specialized leaves of the Venus's-flytrap plant is only triggered by touch, not shaking. The inner surface of this trap has several trigger hairs. These hairs will only activate the closing of the trap if they are touched several times in rapid succession. One touch has no effect. In this way, the trap is only likely to close if an insect is exploring the leaf, but not if the insect flies away after a single contact. Trap clo-

A closed sensitive plant. In an example of thigmonasty, the leaves of the mimosa fold up when they are touched by an animal, perhaps to discourage the animal from eating it.

sure in turn triggers the release of **enzymes** that break down the prey in the trap. Many insectivorous plants grow in bogs where little combined nitrogen (nitrate, nitrite, or ammonia) is available because the water is so acidic that decomposition is slowed. The digestion of the prey in traps is important to the plant because it provides a source of combined nitrogen for protein synthesis.

enzyme a protein that controls a reaction in a cell

The rapid movements of the sensitive plant and the Venus's-flytrap share similar mechanisms. Stimulation causes a wave of electrical signals called action potentials that are similar to, but slower than, nerve impulses in animals. These signals change the **turgor** (water) **pressure** inside cells causing some cells to expand and other cells to contract. After a certain amount of time without any further stimulation, the turgor changes again and the organs open up.

turgor pressure the outward pressure exerted on the cell wall by the fluid within

Thigmonastic movements also help spread seeds. When ripe fruits of touch-me-not plants (impatiens) are touched, they snap open with such force that they spread seeds into areas where the new seedlings will not be shaded by the parent plant. SEE ALSO Carnivorous Plants; Flavonoids; Hormonal Control and Development; Hormones; Plastids; Rhythms in Plant Life.

Fred D. Sack

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COMMON PLANT SPECIES FOUND IN TUNDRA

Sedges (Cyperaceae family)
Carex aquatilis
Carex bigelowii
Eriophorum vaginatum
Eriophorum scheuchzeri

Grasses (Poaceae family)
Poa arctica
Poa alpina
Alopecurus alpinus
Arctophila fulva
Deschampsia caespitosa
Arctagrostis latifolia
Trisetum spicatum

Willows (Salicaceae family)
Salix arctica
Salix rotundifolia
Salix reticulata

Blueberries and Heaths (Ericaceae family)
Vaccinium uliginosum
Vaccinium vitis-idaea
Arctostaphylos alpina
Arctostaphylos uva-ursi
Ledum palustre
Cassiope tetragona
Empetrum nigrum

(continued on page 139)

Tundra

Tundra is treeless vegetation found at high elevation in mountains and in many landscapes of the Arctic. Collectively, **ecosystems** with tundra vegetation are grouped into the tundra biome. A distinction is usually made between Arctic tundra, which exists beyond the northern limit of tree growth, and alpine tundra, which exists above the elevational limit of tree growth in mountains. In mountains of the far north this distinction becomes blurred as tree lines descend to meet the northern limits of trees. Tundra is dominated by low-growing, perennial **angiosperms** and by mosses and lichens. Larger plants include grasses, sedges, herbs, and dwarf shrubs, but it is the lack of trees that most characterizes tundra. Plant species commonly found in tundra include sedges; grasses, including many of the genus *Poa;* willows, blueberries, dwarf birch, and other deciduous and evergreen shrubs or other low-growing woody plants; a host of herbaceous perennials, including many species of the genus *Saxifragra*, many members of the buttercup family, and several members of the rose family.

ecosystem an ecological community together with its environment

angiosperm a flowering plant

Climates of tundra regions are generally cold, and temperatures are commonly below freezing for much of the year, limiting the period of plant growth to a briefly thawed period during summer. Annual precipitation in tundra regions includes snow, although the amount of snow and total precipitation varies tremendously among different areas of tundra. Tundra regions are snow-covered much of the year, but the depth and duration of snow cover differs between locations. The tundra of the Sierra Nevada of California is characterized by heavy winter snow and little summer precipitation, while tundra in the Rocky Mountains generally has less snow but dependable summer rains. Precipitation in tundra regions of the Arctic is generally extremely low, often less than that found in many desert regions, but most soils nonetheless remain moist and may be waterlogged.

It may seem paradoxical that Arctic regions may have less precipitation than many deserts, yet they are covered by moist or wet tundra with numerous ponds and lakes. Low temperatures explain this apparent contradiction, limiting effects of evaporation and contributing to the formation of frost. Soils and materials beneath tundra are considered to be in a permafrost (perennially frozen) condition when they remain frozen for periods of two or more years. Permafrost is a condition generally characteristic of Arctic tundra soils but is also descriptive of isolated portions of the soils of alpine tundra regions. The top of the permafrost layer occurs a few inches to several feet below the surface and can extend downward for many feet. Permafrost soils drain poorly since the frozen soil is as impermeable as rock, and because much of the Arctic landscape is flat. A small amount of precipitation in the Arctic may be held in the thawed soil near the tundra surface, creating a moist landscape dotted with ponds and lakes. The flat Arctic plain is also patterned with irregularly shaped ridges and depressions, called polygons.

aeration introduction of air

Soils of tundra regions are slow to develop due largely to low temperatures and limited periods of thaw. A variety of soil types may develop with time, depending primarily upon moisture or the degree of saturation. Wet tundra, with poor **aeration** and slow decomposition of plant roots, mosses, and other organic matter, produces highly organic soils, while well-drained tundra is characterized by mineral soils. The soil supply of nitrogen, phosphorus, or other elements needed by plants is often low and limits plant growth, and thus tundra regions generally support fewer animals than grasslands and other biomes. Despite low net primary productivity (plant growth potentially available to grazing animals), tundra regions support a variety of mammals, birds, and insects. Arctic tundra herbivores (plant eaters) include caribou, musk ox, lemmings, insects, hares, ground squirrels, and ptarmigan. Carnivores (eaters of insects or other animals) include many birds, especially waterfowl and shorebirds (that appear only in summer), snowy owls, jaegers, and ravens. Other important Arctic carnivores include Arctic fox, wolves, brown bears, and mosquitoes. The fauna of alpine tundra is variable but commonly includes various species of mountain sheep and/or mountain goats, voles and other rodents, bears, eagles, insects, and a variety of animals characteristic of the adjacent forests that sporadically use tundra habitats.

Within both Arctic and alpine regions exist extremes of vegetation considered atypical of tundra. Many areas within the Arctic are true desert; vegetation scientists classify these areas as polar desert. Tropical high mountains exhibit treeless zones at high elevations, sharing many similarities with the alpine tundra of temperate regions, but the lack of seasons, the large **diurnal** temperature variations, and the presence of distinct plant growth forms are clear differences. Tropical alpine vegetation commonly includes one plant life form not found in other tundra regions: the tall columnar rosette. In the tropical alpine of Africa this life form is represented by members of the genus *Lobelia*, in the Andes of South America by members of the genus *Espeletia*, and in high mountains of Java it is represented by tree ferns. The absence of this life form in Arctic and temperate alpine tundra probably reflects the importance of wind in shaping plants of these ecosystems. **Floristic** similarities between tropical alpine and temperate alpine or even Arctic tundra regions include **genera** or species of mosses, lichens, and occasionally **vascular plants** that are held in common.

During glacial periods of the past, much of the area now covered by the Bering Sea was a land mass. This Bering land bridge, connecting North America and Eurasia, allowed plant and animal **populations** to migrate between Northern Hemisphere continents of Eurasia and North America. Today many tundra genera, including both plants and animals, have circumpolar distributions (surrounding the northern parts of the world). Since species migrations were made possible during the cold periods of the Pleistocene with lowered sea levels due to great masses of ice on land, tundra-like vegetation formed over great expanses in the Northern Hemisphere. Today isolated alpine regions show remarkable similarities in flora and fauna to those of the Arctic echoing a common tundra heritage. SEE ALSO BIOGEOGRAPHY; BIOME.

Kim Moreau Peterson

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COMMON PLANT SPECIES FOUND IN TUNDRA

(continued from page 138)

Dwarf birch *Betula glandulosa*
Herbaceous perennials
Saxifrage family
- *Saxifragra oppositifolia*
- *Saxifragra cernua*
- *Saxifragra caespitosa*

Ranunculaceae (Buttercup family)
- *Ranunculus nivalis*
- *Anemone parviflora*
- *Caltha leptosepala*

Rosaceae (Rose family)
- *Geum Rosii*
- *Dryas integrifolia*
- *Potentilla* species
- *Rubus* species

Brassicaceae (Mustard family)
- *Draba* species

Artemisia species
Lupinus species
Castilleja species
Pedicularis species
Senecio species
Silene species

diurnal daily, or by day

floristic related to plants

genera plural of genus; a taxonomic level above species

vascular plants plants with specialized transport cells; plants other than bryophytes

population a group of organisms of a single species that exist in the same region and interbreed

Sedges on the tundra in Brooks Rouge, Alaska.

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Turf Management

Careers in turf management involve working outdoors with plants, people, and Mother Nature. Turf managers are employed at various turfgrass facilities worldwide. Although advancement into a management position normally requires a two- or four-year college degree, there are various nonmanagement positions for those who choose not to attend college. Below are various career opportunities in the turf management industry.

A golf course superintendent supervises the maintenance of a golf course. Depending on the course, the superintendent may oversee two to more than fifty employees with a budget ranging from $100,000 to over $1,000,000. Some superintendents enjoy the challenge of hosting a professional golf tournament or building a new course, while others enjoy the more relaxed atmosphere of a daily-fee public course. Salary range for head superintendents was $35,000 to $150,000 in 1999. Graduates with a two- or four-year degree in turf management start their careers as a first or second assistant superintendent. Starting salaries ranged from $25,000 to $35,000 in 1999. Advancement to head superintendent can occur within one to five years.

A sports turf manager oversees the maintenance of one athletic field or an entire sports complex. Professional sports facilities need educated turf managers to maintain the fields used by professional baseball, football, and soccer teams. Universities, colleges, high schools, community parks, horse tracks, polo clubs, tennis clubs, and cricket clubs are beginning to recognize the need for a professional turf manager to maintain their athletic complexes. A well-maintained field reduces injuries and offers better playing conditions. Graduates with a two- or four-year degree in turf management usually start their careers as an assistant field manager. Some may even start as head field manager. In 1999 salaries ranged from $25,000 to $80,000.

Lawn care managers often work as supervisors, consultants, or technicians for professional lawn care franchises. Many start their own company. Responsibilities can include mowing, fertilization, pest control, renovation, sales, and evaluation of home lawns. College graduates normally start as technicians or managers. Lawn care is the largest sector of the turf industry. Homeowners in the United States spend about $15 billion on their lawns and landscape each year.

A grounds manager maintains an institutional site landscaped with turf, trees, flowers, buildings, and roads. They can be hired by colleges, universities, municipalities, park and recreation facilities, office parks, residential communities, hotels, resorts, theme parks, and cemeteries. Education in turf management, landscaping, ornamentals, and business is helpful.

Sod producers grow, harvest, and sell mature turfgrass to various customers. Customers include homeowners, landscapers, golf courses, and athletic fields. Many producers own and operate their own sod farms. Sales and service people also sell and/or service the materials and equipment that turf managers use. Indeed, there are sales and service representatives associated with just about anything purchased in the turf industry—mowers, fertilizer, pesticides, seed, sprayers, and **amendments**. Education and experience in turf management and related fields is helpful.

amendment additive

Researchers and educators develop the grass or fertilizer of the future. They teach turf management at a technical school, college, or university as well. Consultants give turf advice in exchange for money. Clients include homeowners, golf courses, athletic fields, institutions, and landscape management companies. SEE ALSO Economic Importance of Plants; Grasses.

Douglas T. Linde

V

Vacuoles

Vacuoles are **organelles** of plant, fungal, and algal cells. They are part of the internal membrane system and are separated from the rest of the cytoplasm by a membrane called the **tonoplast**. A single large vacuole occupies more than 80 percent of the volume of most plant cells, mature fugal hyphae, and some algal cells. Many smaller vacuoles are found in expanding plant cells and in the tips of growing fungal **hyphae**. These vacuoles can be less than one micrometer in diameter. As the cell in which they reside matures, smaller vacuoles fuse to produce larger vacuoles.

Vacuoles are multifunctional organelles, and individual cells may contain more than one kind of vacuole, each kind having a different function. Vacuoles play crucial roles in cell expansion, serve as storage compartments for nutrients, and function as **lytic** organelles that contain digestive **enzymes**. **Compounds** contained within vacuoles also protect cells against environmental damage and deter attack by **herbivores**.

organelle a membrane-bound structure within a cell

tonoplast the membrane of the vacuole

hyphae the threadlike body mass of a fungus

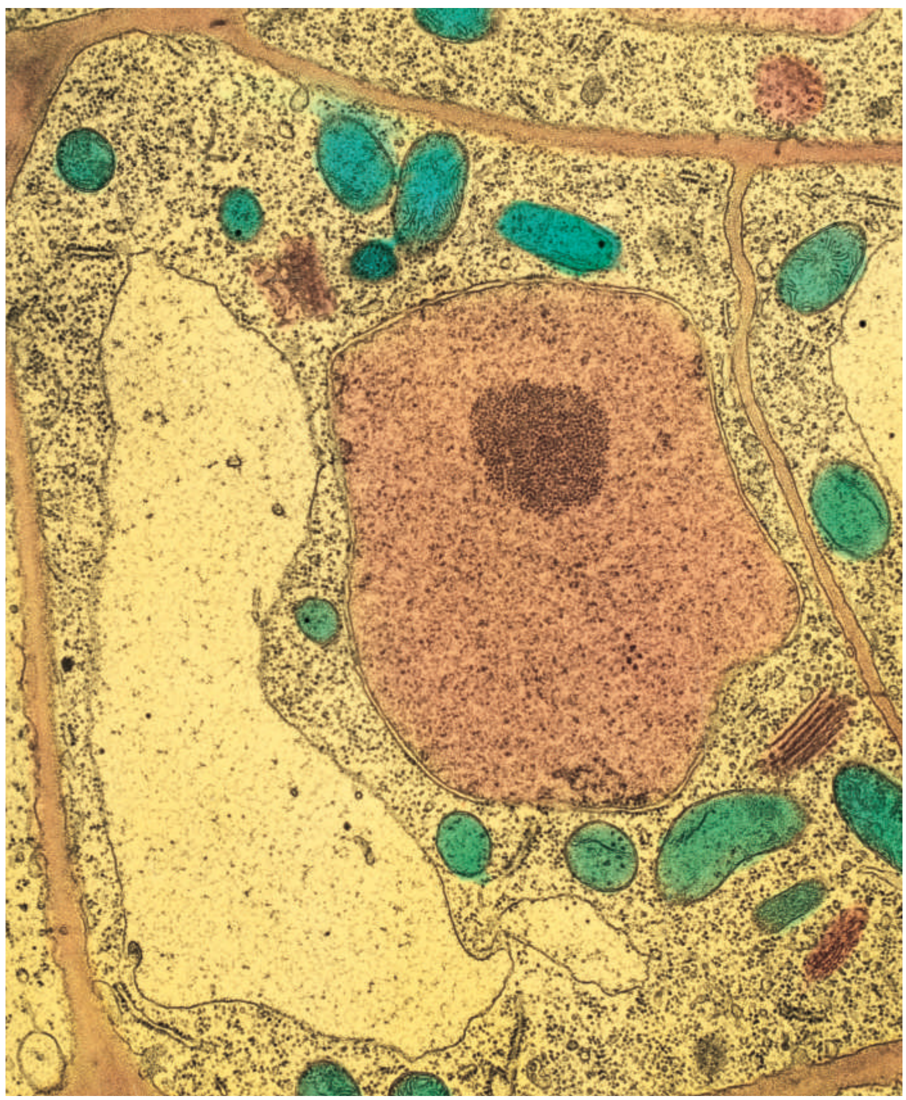
lytic breaking apart, by the action of enzymes.

enzyme a protein that controls a reaction in a cell

compound a substance formed from two or more elements

herbivore an organism that feeds on plant parts

turgor pressure the outward pressure exerted on the cell wall by the fluid within



An electron micrograph of a young cell from the root-tip meristem of *Arabidopsis thaliana.* The nucleus (pink) contains a nucleolus (dark) and granular nucleoplasm; the cytoplasm contains mitochondria (blue), proplastids (juvenile chloroplasts; green), and Golgi bodies (red). The large L-shaped body on the left (gold) and the smaller body to the right at its base are vacuoles.

Vacuoles take up water through specialized membrane transporters called aquaporins. The hydrostatic pressure that develops within each cell, known as **turgor pressure**, is required for cell expansion and growth. Turgor pressure is carefully regulated in plants, fungi, and many algae by controlling rates of water and ion movement through the tonoplast. In fresh water algae and fungi lacking cell walls, **contractile** vacuoles fill with excess water from the cytosol and their contents are expelled from the cell through specialized pores.

The vacuole is an acidic organelle, and the **pH** of most vacuoles is around 5 to 6. Vacuole acidity is important for its lytic function since many vacuolar enzymes work most efficiently at or near pH 5. Acidification of vacuoles is brought about by transporters embedded in the tonoplast. These transporters use the energy stored in adenosine triphosphate (**ATP**), or in some cases, pyrophosphate, to pump protons from the cytosol into the vacuole. In extreme cases, such as in the lemon fruit juice sac, the pH of the vacuole can be as low as 2.

Vacuoles store organic acids, carbohydrates, proteins, and minerals. Some of these compounds are important for human nutrition. These include proteins stored in the cotyledons of beans and peas or the grains of cereals; simple sugars such as sucrose found in many fruits, the stems of sugarcane and the roots of sugar beets; and minerals such as potassium. In the leaves and stems of forage grasses, vacuoles store complex **polysaccharides** that are the principal energy source for herbivores.

Many other compounds accumulate in vacuoles. These include the water-soluble anthocyanin **pigments** that give the blue or red color to red beets, grapes, and peonies. Anthocyanins are also contained in the vacuoles of leaves and stems and are important **photoprotectants** that absorb excess light. **Alkaloids**, enzyme inhibitors, and **toxins** are contained in some vacuoles. Although these compounds may deter herbivory, some have been used to produce medicines. Aspirin and morphine are two examples. Waste products and **xenobiotics**, including herbicides, are often shuttled into vacuoles by specialized membrane transporters. Once in the vacuole, these compounds are digested or detoxified. SEE ALSO ANTHOCYANINS; CELLS.

Paul Bethke and Russell Jones

contractile capable of contracting

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral; low pH numbers indicate high acidity; high numbers indicate alkalinity

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

polysaccharide a linked chain of many sugar molecules

pigments colored molecules

photoprotectants molecules that protect against damage by sunlight

alkaloids bitter secondary plant compounds, often used for defense

toxin a poisonous substance

xenobiotics biomolecules from outside the plant, especially molecules that are poten

van Helmont, Jan

Flemish Physician and Chemist

1579–1644

Renowned physician and chemist Jan van Helmont was born into the Flemish gentry in 1579. He received his medical degree at the age of twenty, then proceeded to revolutionize the field of plant nutrition. As a young university student first in Belgium, then in Switzerland, France, and England, van Helmont openly rejected the mysticism and superstition prevalent in academia at the time, being especially skeptical of natural magic and magnetic cures.

Jan van Helmont.

In all of his attempts to understand "the small things" that at the time were treated with "magic" and magnetism and today are studied with microscopes, van Helmont relied on the principles of balance, experiment, and quantification. Van Helmont applied chemical analysis to smoke, which he produced by burning a variety of solids and fluids. He observed that the vapors that formed when solids were burned were very different from "just air"; these vapors had distinct and unique properties depending on the solid from which they had been derived.

Van Helmont called this class of vapors by the term "gas." He referred to gas as being "wild," stating that this new type of substance "could not be contained by vessels nor reduced into a visible body." Van Helmont described and identified a variety of gases and therefore is credited as the "discoverer" of gas.

quantitative numerical, especially as derived from measurement

Van Helmont's desire to understand the composition of water initially motivated his experiments on plant nutrition. He was the first to use a **quantitative**—and ingenious—experimental approach to show that plants obtain nutrition from the chemicals in water. Van Helmont planted a young willow plant in a container. The willow shoot weighed 5 pounds and the container (including earth) had a dry weight of 200 pounds. For five years, van Helmont attended his willow plant with great care, watering it as often as necessary. Once those five years were up, van Helmont weighed the shoot. It had gone from 5 pounds to 169 pounds. Meanwhile, the dry weight of the soil had decreased by only 2 ounces. As van Helmont concluded: "Therefore 164 pounds of wood, bark, and root have arisen from water alone." Van Helmont thus demonstrated that the main source of plant nutrition was not the soil, thus countering a widely held belief among his contemporaries.

Ironically, van Helmont, even though he was extremely interested in the air, overlooked the role that air plays in plant nutrition. He had the right idea, but came to the wrong conclusion. It is known now that plants need to get nutrients from water and air in order for carbon fixation to occur.

Van Helmont's radical thinking would eventually land him in some trouble with the Spanish government and Catholic church. In 1625 the General Inquisition of Spain condemned a treatise he had published in 1621, citing van Helmont for 157 counts of heresy, impudence, and arrogance, as well as for association with Lutheran doctrine. He was kept under house arrest for years, and, perhaps because of this experience, published little of his work. When he was dying in 1644, he asked his son to edit and publish his works. SEE ALSO PHYSIOLOGIST; PHYSIOLOGY; PHYSIOLOGY, HISTORY OF; WATER MOVEMENT.

Hanna Rose Shell

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van Niel, C. B.

Dutch Microbiologist and Educator

1897–1985

Cornelis Bernardus van Niel was a Dutch microbiologist whose experiments with bacteria helped explain how photosynthesis occurs in plants. Sulfur bacteria particularly interested van Niel, because there was a controversy in the early 1900s concerning the bacteria. Scientists were not sure if the bacteria got their energy from chemicals in their environment or from sunlight. They knew that the bacteria used sulfur **compounds** and did take in carbon dioxide to create more complex carbon compounds, and van Niel wanted to determine which energy source the bacteria used to do this.

compound a substance formed from two or more elements

One problem was that previous scientists had usually studied cultures of bacteria that contained several different species. They knew that the bacteria needed light and also needed and stored sulfur compounds, but the interactions between different species in the cultures made experimentation difficult. Van Niel decided he would have to do his work on pure cultures. He began the labor of isolating and studying pure cultures of purple and green sulfur bacteria in the Netherlands and he continued this work after he transferred to the Hopkins Marine Station in California, in 1929.

Van Niel carefully examined his cultures, using very specific growing conditions. He measured as accurately as possible the amounts of carbon, sulfur, and other chemicals that the bacteria used up or released. In this way, he saw that in the light, the amount of carbon dioxide the bacteria could convert into other carbon compounds depended precisely on how much hydrogen sulfide was available. He worked out a formula for this bacterial photosynthesis and he noticed it was very similar to the formula known for plant photosynthesis. The only difference was that the bacteria used hydrogen sulfide in the reaction where plants used water, and the bacteria produced sulfur compounds where the plants produced oxygen. This led him to make a general formula for the reactions of photosynthesis in both bacteria and plants that is still used today.

The most striking part of van Niel's ideas about photosynthesis was that light was used to split water or hydrogen sulfide. The energy and hydrogen released would then be used to reduce carbon dioxide into more complex compounds. This was new and interesting at the time, because it meant that the oxygen given off by plants during photosynthesis came from the split water molecule, and not from carbon dioxide as previously thought. Later researchers confirmed van Niel's theory by doing experiments using heavy isotopes of oxygen to label the oxygen and observe its origins in photosynthesis. Van Niel's research originated the study of the electron transport chain involved in transferring the energy in photosynthesis.

Other van Niel studies became the foundation for studying bacterial evolution and for the classification of organisms as **prokaryotes** or eukaryotes. Van Niel died in 1985. SEE ALSO PHOTOSYNTHESIS, LIGHT REACTIONS AND; PHYSIOLOGIST; PHYSIOLOGY; PHYSIOLOGY, HISTORY OF.

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

Jessica P. Penney

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Variety

population a group of organisms of a single species that exist in the same region and interbreed

Plant species maintain different levels of variation within and among **populations**, much of which is genetically determined. As such, variation in form below the taxonomic rank of species, called infraspecific variation, is widely recognized in plants. In contrast to zoological taxonomy, three categories have been applied to recognize this variation in plants. In order of decreasing taxonomic rank, these are: subspecies, variety, and forma. Additionally, the category of cultivar is used to recognize horticultural varieties not typically found in naturally occurring populations. The subspecies, which is the most inclusive of the three categories, is usually applied in recognition of population variation that is correlated with geography. By definition, populations of subspecies differ from other such populations. Furthermore, subspecies are expected to interbreed more freely than species, which may comprise two or more subspecies. The category of variety is similarly applied to recognize variation below the level of subspecies. Unfortunately, the two categories are not distinct, and application of the taxonomic rank of variety is more frequently encountered. Forma, the least-inclusive category, is applied to recognize minor infraspecific variation that is presumably due to variation at a single gene and, as such, may vary within populations. Flower color variants are typically recognized at this level. SEE ALSO Clines and Ecotypes; Cultivar; Species; Taxonomy.

Leo P. Bruederle

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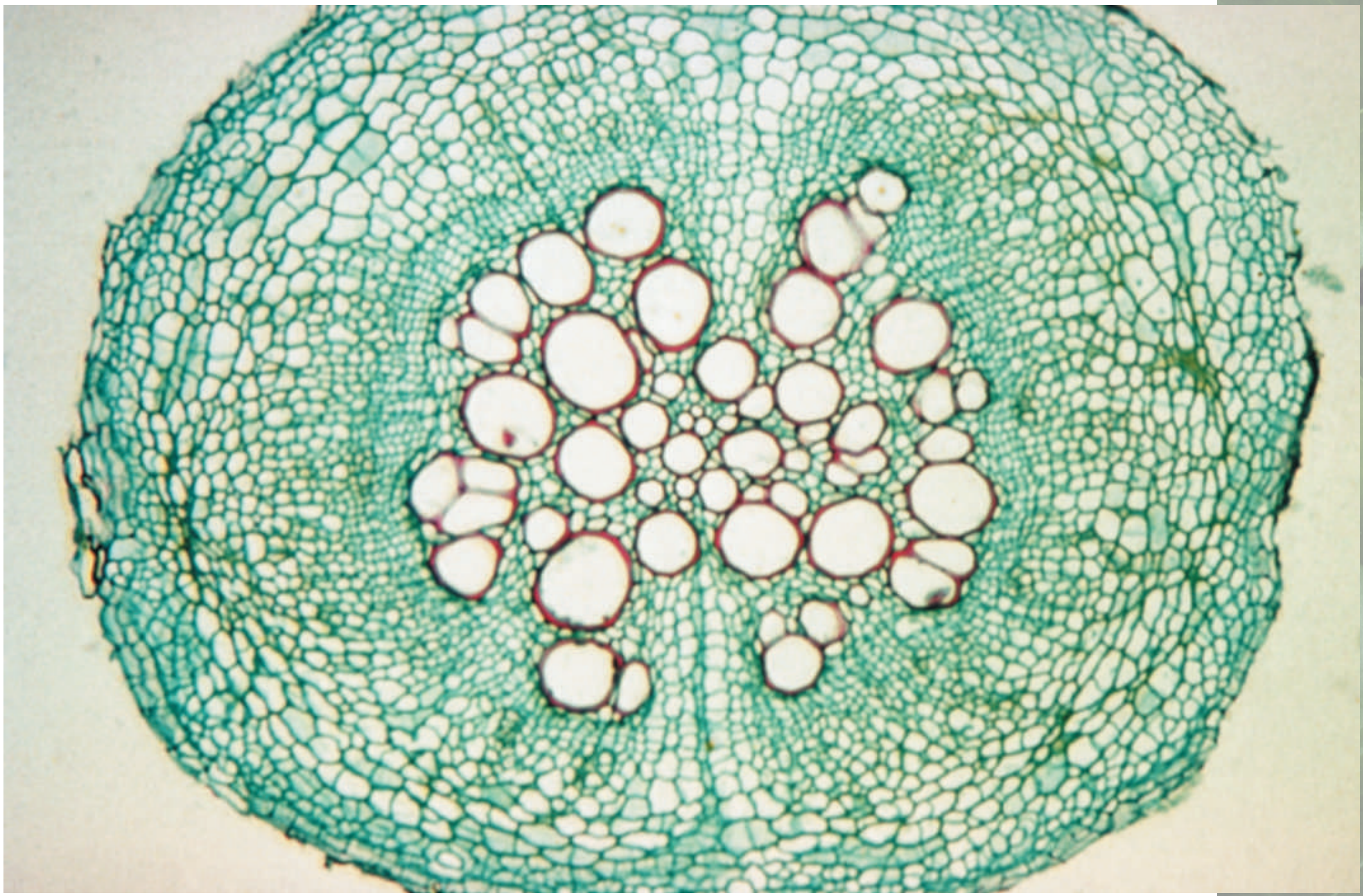
Vascular Tissues

All living cells require water and nutrients. If an organism is a single cell or if its body is only a few cells thick, water and nutrients are easily moved through the organism by diffusion. However, diffusion is generally too slow for even small plants to meet their water and nutrient needs. In plants, this problem was solved with the evolution of a specialized system for fast and efficient long-distance transport of water and nutrients. This specialized cellular network is the vascular tissue system; plants with vascular tissues are referred to as vascular plants.

The vascular tissue system is composed of two different types of tissues: xylem and phloem. Although both xylem and phloem form a continuous tissue system throughout the plant body, the two tissues have different functions. Xylem is the primary water- and mineral-conducting tissue, and phloem is the primary food-conducting tissue.

Unlike the circulatory system in animals, the vascular tissue in plants does not recirculate water. Instead, water takes a one-way journey from the



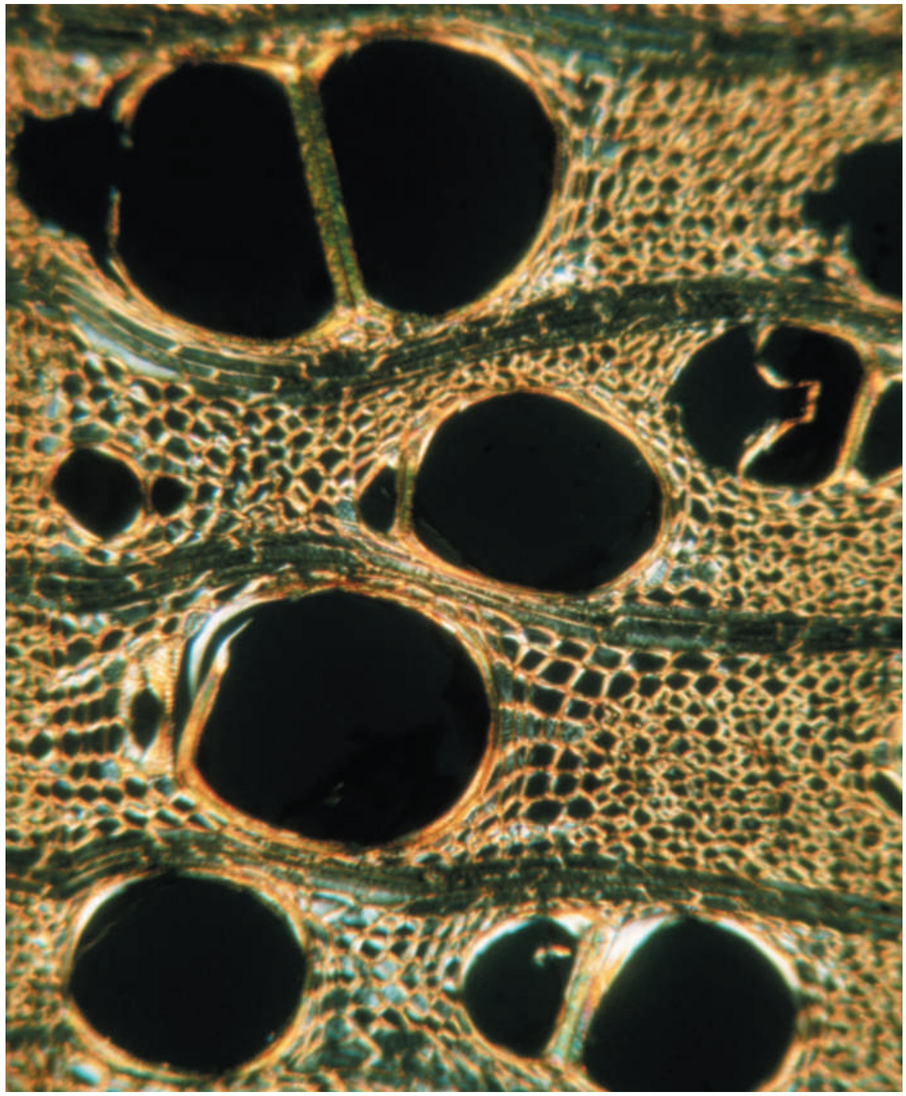
Cross-section of a carrot root tissue, showing xylem, phloem, and cortex cells.

soil upward through the plant body to be lost to the atmosphere through evaporation. The watery journey occurs within the xylem tissue. In contrast, phloem tissue transports dissolved sugars (food) from regions where sugars are made or stored (sources) to regions where sugars are required for metabolic processes (sinks). Phloem transports sugars from source to sink. Source sites include photosynthetic tissue, usually leaves, where sugars are manufactured, and storage organs (thickened stems or roots, such as the root of a sugar beet).

Vascular Plants

Freed from the requirement to hug a moist soil surface, plants with vascular tissue can grow tall, extending their complex stems and leaves into the dry air. Vascular tissue, along with several other important plant features, allowed plants to colonize Earth's surface. Today, our planet hosts an enormous diversity of vascular plant life, including such different forms as ferns, redwood trees, oak trees, and orchids.

Vascular tissue develops in all organs—root, stem, and leaf—of the plant body. In the primary plant body, vascular tissue differentiates from a primary meristem, the procambium. Xylem and phloem tissues that differentiate from procambial tissue are called primary xylem and primary phloem. In plants with secondary growth, vascular tissue differentiates from a lateral meristem, the vascular cambium, producing secondary xylem and secondary phloem. Secondary xylem is a familiar product: wood.



The xylem bundles of a cross-section of teak wood magnified fifty times.

Xylem: The Water-Conducting Vascular Tissue

parenchyma one of three types of cells in ground tissue

tracheid a type of xylem cell for water transport

Xylem is a complex tissue composed of several different cell types. This tissue includes **parenchyma** cells, fibers, and two cell types specializing in water and mineral transport: **tracheids** and vessel members. Collectively tracheids and vessel members are called tracheary elements.

The tracheid evolved first, appearing in the fossil record about 420 million years ago, long before vessel members. Most seedless vascular plants, such as ferns, and cone-bearing seed plants, such as pines, have tracheids only. Although vessel members evolved independently several times and are present in a few seedless vascular plants, vessel members are usually associated with flower-bearing seed plants.

Tracheids are less specialized than vessel members. Tracheids appear first in the fossil record; vessel members and fibers are thought to have derived from tracheids. The less-specialized tracheid provides both water-conducting and strenghtening traits in one cell. In plants with fibers and vessel members, fibers specialize in strengthening plant tissue and vessel members specialize in water conduction.

Development. Mature tracheary elements are dead, tubelike cells. Only cell walls remain intact at the end of the differentiation process; the **protoplast** is completely eliminated, leaving a hollow cell. Whether tracheary elements arise from **meristematic** cells of the procambium or later in development from the vascular cambium, the pattern of tracheary element development and maturation is similar.

protoplast the portion of the cell within the cell wall

meristematic related to cell division at the tip

One of the first indications that a meristematic cell will become a tracheary element is cell elongation; mature tracheary elements are longer than they are wide. The elongating cells have thin, primary cell walls; but, as the cells elongate, additional cell wall **compounds** are deposited to the inside of the primary wall. The additional wall deposition forms the secondary cell wall. One of the secondary wall compounds is a complex **polymer** called lignin. A **lignified** cell wall is impermeable to water. To allow for water transport from cell to cell, numerous regions of the primary cell wall remain free of secondary wall deposition. The regions lacking secondary walls are called pits. Pit structure and the pattern of pitting on the walls of tracheary elements are specific for different plant species and are useful traits in plant identification.

compound a substance formed from two or more elements

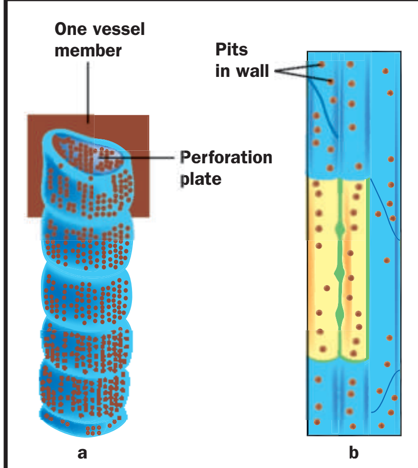
polymer a large molecule made from many similar parts

lignified composed of lignin, a tough and resistant plant compound

Water Flow in Tracheary Elements. The pits of adjacent cells are aligned with one another, allowing water to pass from tracheary element to tracheary element. Water passes through aligned pits because the two adjacent primary walls, and the middle **lamella** cementing the two cells together, are composed of complex carbohydrates permeable to water, such as cellulose and pectin. An aligned pair of pits is called a pit pair, and the primary walls and middle lamella of the pit pair are called a pit membrane.

lamella a thin layer or plate-like structure

Although pit membranes are permeable to water, they do offer some resistance to the flow of water between cells. In vessel members, the maturation process includes dissolution of the end walls to form perforation plates. Perforation plates are cell wall regions that are completely open, offering no resistance to water flow. Vessel members are connected end-to-end, forming tubes called vessels. Water taken into a vessel from surrounding parenchyma cells, tracheids, or other vessels must pass through pits in the lateral walls of the vessels; but, once inside a vessel, water can flow unimpeded for the length of that vessel.



Xylem conducting cells. (a) A vessel composed of several vessel members; pits occur in the lateral walls and a perforation plate is visible in an end wall of one of the vessel members. (b) Adjacent tracheids; pits occur on lateral and end walls. Redrawn from Rost et al., 1998, Figure 4.11.

Because vessel members lack end walls, moving water with less resistance, they are thought to be more efficient water-conductors than tracheids. However, there is a tradeoff. If an air bubble forms in a vessel, it can expand and fill the entire vessel. An air-filled vessel can no longer function in water transport. Because water must pass through the pit membranes of pit pairs when traveling from tracheid to tracheid, air bubbles cannot pass between adjoining tracheids. Pit membranes are effective barriers to air bubbles, trapping bubbles within a single tracheid.

Secondary Wall Reinforcement. In primary xylem, selective secondary wall deposition creates different cell wall patterns in tracheary elements. In the first formed tracheary elements of the primary xylem, secondary wall deposition tends to occur in ringlike (called annular) or helical (spiral) bands around the cell. As the primary plant body continues to lengthen, cells with annular or helical thickenings stretch. These cells are often stretched beyond functional usefulness. Later, but still during primary growth, ladder-like (scalariform), netlike (reticulate), or pitted secondary wall patterns may develop. With increasing amounts of secondary wall deposition, tracheary elements become stronger and less resistant to stretching. Therefore, scalariform, reticulate, and pitted tracheary elements are generally found in organs that have ceased elongation.

The lignified secondary walls and pit pairs of tracheary elements and the perforation plates of vessel members provide for efficient water-conduction through vascular tissue. Water and dissolved minerals taken in from the external environment—usually wet soil—move upward through the xylem tissue of roots into stems and finally into leaves. Within leaves, water evaporates from cell surfaces and is lost to the environment as water vapor. Water evaporation from a plant surface is called transpiration. Water is literally pulled up tracheary elements during transpiration. The evaporation-generated pulling stretches hydrogen bonds between connected water molecules, resulting in a column of water that is under tension (negative pressure). The lignified cell walls of tracheary elements are strong enough to resist the tension, preventing inward cell collapse during water movement.

Phloem: The Food-Conducting Vascular Tissue

Phloem tissue is a complex tissue consisting of parenchyma cells, fibers, and one of two types of food-conducting cells. Sieve-tube members and sieve cells are food-conducting cells and are collectively called sieve elements. Sieve-tube members connected end-to-end form a sieve tube. Sieve cells evolved before sieve-tube members and are less specialized. Cone-bearing seed plants have sieve cells, and the more advanced flowering seed plants have sieve-tube members.

Sieve elements are long, narrow cells with primary cell walls. During differentiation, a sieve element undergoes major **protoplasmic** changes, including loss of its nucleus and vacuolar membrane. In addition, the cell loses ribosomes, the Golgi complex, and the cytoskeleton system, but the cell membrane remains intact. Next to the cell membrane, a network of smooth **endoplasmic reticulum** lines the cell, and a few plastids and **mitochondria** remain intact.

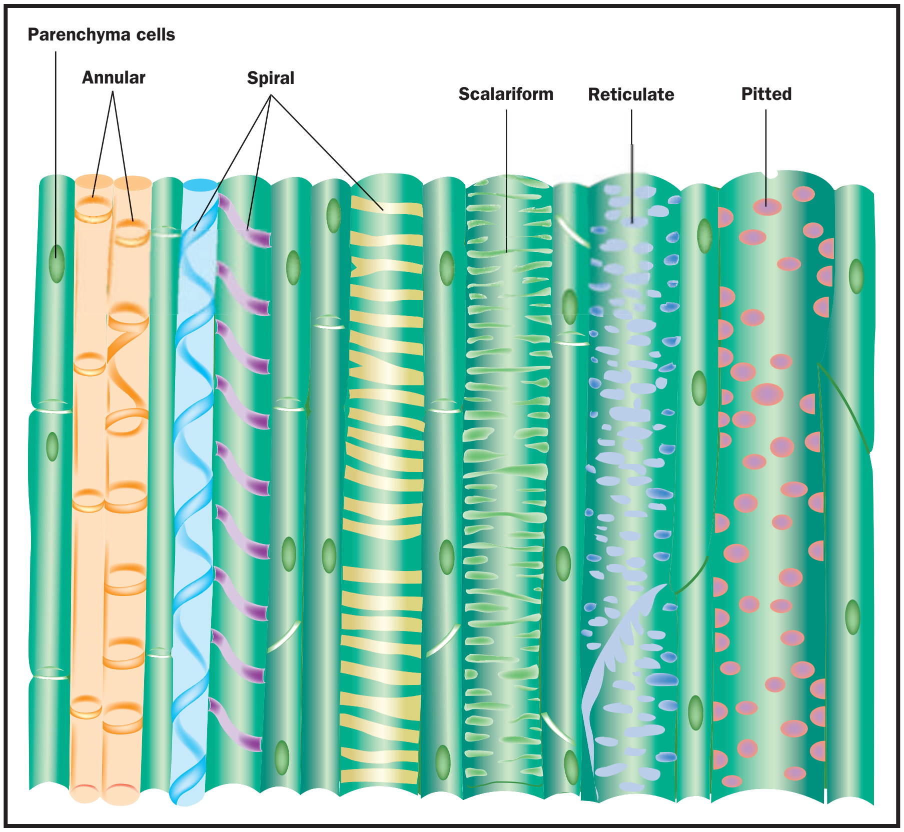
protoplasmic related to the protoplasm, cell material within the cell wall

endoplasmic reticulum membrane network inside a cell

mitochondria cell organelles that produce ATP to power cell reactions

Sieve Areas. The defining feature of sieve elements are sieve areas. A sieve area is a cluster of pores in the wall of a sieve element. These pores allow materials to flow from cell to cell. In sieve cells, end walls overlap and, although sieve areas are found on all wall surfaces, they are concentrated on overlapping wall regions. Sieve-tube members have two types of sieve areas. Sieve plates are a specialized type of sieve area with relatively large pores. Most sieve plates occur on end walls of sieve-tube members with relatively smaller-pored sieve areas on the lateral cell walls. Sieve plate complexity is variable. Some sieve-tube members have compound sieve plates with several sieve areas on a steeply inclined end wall. Sieve-tube members with compound sieve plates are considered less specialized than sieve-tube members with simple sieve plates and horizontal end walls. The pores of simple sieve plates are relatively wider than the pores of compound plates, and wider pores increase cell-to-cell connection.

Unlike tracheary elements of the xylem, the fluid contents of sieve elements in the phloem are under positive pressure, and the movement of sugars and other substances through sieve elements is directed by pressure dif-



Patterns of secondary wall deposition in tracheary elements. Cells with annular and spiral secondary wall thickenings can stretch during organ elongation. As organ elongation slows and then ceases, the wall thickening patterns tend to grade from scalariform and reticulate to pitted. Redrawn from Rost et al., 1998, Figure 4.9.

ferences. Because cell contents are under pressure, sieve elements require a method of sealing cells to prevent the loss of cellular contents upon sieve element injury or death. One blocking substance is callose. Callose is a carbohydrate that lines the pores of sieve areas and sieve plates; it can rapidly expand, filling pores and blocking the loss of cell contents. A few flowering plant sieve-tube members contain a protein substance called P-protein. (The "P" is for phloem.) P-protein appears to line sieve plate pores in living cells and to plug pores of damaged cells. Although the function of P-protein is not known, it may serve as an additional method of blocking sieve pores and preventing the loss of cell contents upon injury.

Companion Cells and Albuminous Cells. There are two types of specialized cells associated with sieve elements. Sieve-tube members are always associated with companion cells. Both cells arise from the same meristematic cell and are joined by numerous, well-developed **plasmodesmatal** connections. Companion cells probably provide a delivery and support system for the nonnucleated sieve-tube members. Associated with sieve cells are specialized parenchyma cells called albuminous cells. Albuminous cells may perform the same function for sieve cells as companion cells do for sieve-tube members.

albuminous gelatinous, or composed of the protein albumin

plasmodesmata cell-cell junctions.

Nonvascular Plants

Most organisms that we automatically classify as plants, such as roses and corn, have a vascular tissue system and are called vascular plants. However, plants such as mosses lack this highly developed transport system and are classified as nonvascular plants.

Informally, nonvascular plants are called bryophytes, and include three groups of plants: liverworts, hornworts, and mosses. Nonvascular plants specialize in absorbing moisture by efficiently moving water over their surfaces through capillary action. In many of these small plants, there is an additional internal conducting tissue that allows for efficient water and food conduction. When present, bryophyte-conducting tissue consists of two specialized cell types: water-conducting hydroids and food-conducting leptoids. Hydroids are elongated cells with thin primary cell walls and no protoplast at maturity. Leptoids are elongated cells, but their lateral cell walls are thick. The end walls of leptoids contain numerous plasmodesmata that may enlarge to form small pores. At maturity, the nuclei of leptoids degenerate. Because bryophyte conducting tissue apparently lacks lignin, it is not considered true vascular tissue. SEE ALSO Anatomy of Plants; Cells, Specialized Types; Roots; Tissues; Translocation; Water Movement.

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Vavilov, N. I.

Russian Geneticist
1887–1943

N. I. Vavilov.

Nikolay Ivanovich Vavilov was a geneticist and **phytogeographer** in Russia. He is best known for his attempts to apply the new science of genetics to improve agriculture in Russia, for his novel theory to determine the centers of origin of cultivated plants, and for his tireless efforts to organize science in Russia. Vavilov is also known as one of the outstanding victims of Soviet oppression during the regime of Josef Stalin. He openly opposed the teachings of the antigeneticist Trofim Lysenko. As a result Vavilov was unjustly imprisoned for supporting the very same work in genetics that had made him famous.

phytogeographer a scientist who studies the distribution of plants

Early Life and Career

Vavilov was born in Moscow on November 25, 1887. He was the oldest of four children born to a wealthy Moscow merchant family. His younger brother, Sergey, shared some of his scientific interests and became a well-known physicist and president of the Soviet Academy of Sciences.

From an early age, Vavilov had an interest in applied botany and agriculture. In 1906 he graduated from a commercial high school and entered the Moscow Agricultural Institute. Following graduation in 1911, Vavilov remained with the head of the department of special agriculture to prepare for an academic career. In 1912 he moved to St. Petersburg, where he worked at the Bureau of Applied Botany of the Ministry of Agriculture and at the

Bureau of Mycology and Phytopathology. The pivotal moment in his early career came when he was sent to study genetics in England. He left for England in 1913 to study with the eminent geneticist William Bateson. He also worked with the geneticist R. C. Punnett and cereal breeder R. D. Biffen. He returned to Russia just after the outbreak of World War I to complete the thesis for his master's degree titled "Plant Immunity to Infectious Diseases." In 1917 he became professor of agriculture, botany, and genetics at the University of Saratov.

Vavilov rose to prominence shortly following the Russian Revolution. He drew the favorable attention of Lenin and was placed in charge of the Bureau of Applied Botany in St. Petersburg. Under his direction, it became one of the world's most active research institutions. By 1934 it had a staff of approximately twenty thousand persons and was known as Lenin's All-Union Academy of Agricultural Sciences. His success was recognized both at home and abroad. Though he was never a Communist, he was made a member of the Soviet Central Executive Committee. He occupied many important international positions including being named President of the International Congress of Genetics in 1939.

Vavilov's Scientific Work

Vavilov's actual contributions to science were unusual. He did not make any new discoveries or formulate new scientific principles but was instead actively concerned with the application of the new genetics to problems of systematics and agriculture. His work fell into three distinct areas, which had in common a concern with cultivated plants.

His earliest work was concerned with the manner in which plants developed immunity to disease. He developed the concept of degree of specialization. This was based on his observation that the wider the range of hosts of a parasitic fungus, the less likely it is that there will be resistant varieties in any of the host species. In other words, the more hosts that were available, the less likely resistance could develop in any one species. In understanding the mechanism by which this happens, Vavilov sought out new varieties of wheat to test for disease resistance. In the process he discovered an important new disease-resistant wheat species, *Triticum timopheevi*, which is still used in breeding for disease resistant stocks. The techniques that Vavilov developed for testing disease-resistance are still important tools for plant disease specialists, or plant pathologists.

His second area of research led to the formulation of the law of homologous series in variation. This law held that genetic and **morphological** regularities existed in the differentiation of species, **genera**, and families. Such parallel variations, he argued, could be found in all categories of classification. Vavilov recognized that the study of similarities in related species and genera could lead to a valuable analytical tool because it could determine if and where any gaps in series of forms existed. Once this was determined, it was then possible to search for the organism that would fit into such a gap. Vavilov closely studied the parallel variation in many forms, especially the cereals, and in the process amassed an enormous amount of data on this economically important group. He was also able to locate many "missing" forms that were expected if his law held true.

morphologically related to shape or form

genera plural of genus; a taxonomic level above species

Vavilov was best known for his third area of research into the origin and distribution of cultivated plants. He built on the earlier work of the French geographer Augustin de Candolle, which had used a novel combination of archaeological, historical, linguistic, and botanical evidence to trace the location of origin of cultivated plants. Vavilov additionally applied the insights and methods from two new sciences, **cytology** and genetics, and traveled extensively to examine and collect close relatives of important cultivated plants. From this work, he derived his own theory of the origin of cultivated plants, which postulated that there were eight principal "centers of origin." According to Vavilov these regions had a broad range of environmental conditions that gave rise to diverse natural floras. Cultivated plants in these regions also had many diverse varieties. Vavilov's novel insight here was to determine that cultivated plants in his centers of origin showed a marked increase in the frequencies of dominant genes compared to plants outside these centers. This, in fact, became his principal criterion for fixing centers of origin. In contrast, cultivated plants outside the centers of origin tended to have much less genetic variability.

cytology the study of cell structure

Vavilov's centers of origin was a provocative and influential theory for its day. Although the specifics of the theory and the actual centers of origin have been called into question, it opened the way for subsequent research. In the process much was understood about the genetics of cultivated plants and many new varieties were collected and introduced.

Much of Vavilov's research over his life was based on close study of geographic distribution and variation. He traveled widely all over the world, but especially in Asia both to examine and collect usually wild relatives of cultivated plants. His expeditions were organized on a grand scale and led to the collection of an enormous range and number of plant **specimens**. Many of his collections of cultivated plants were without counterpart and still remain unsurpassed in quality and number. For his research into the origin of wheat alone, he amassed over twenty-five thousand specimens of different varieties of wheat and its wild relatives. With good reason, Vavilov had been called the most widely traveled biologist of his day.

specimen object or organism under consideration

Vavilov and Stalinist Science

Vavilov rose to such prominence that he was the most visible promoter of science in the Soviet Union. He was an advocate of international collaboration and sought to bring the methods and insights of the new science of genetics from Britain and the United States to improve agriculture in the new Soviet system. Unfortunately, this made him an easy target of anti-Western ideology that gained strength under Stalin's regime. Vavilov's support of Western science generally, and genetics in particular, were openly challenged by Trofim Lysenko, one of the most destructive influences in Soviet science. Although he had no training in the field, Lysenko pretended to be an authority in agricultural genetics. He was opposed to Mendelian genetics and Darwinism but instead was an advocate on **Lamarckian inheritance,** which was more compatible with Soviet ideology. Beginning in the late 1920s, Lysenko and his supporters began to systematically purge the Soviet Union of geneticists who they viewed as slaves to foreign science, as well as anyone who opposed Soviet ideology. Many of the leading geneticists in the Soviet Union were exiled, imprisoned, dispersed, or exe-

Lamarckian inheritance the hypothesis that acquired characteristics can be inherited cuted. By the late 1930s Vavilov had been relieved of his administrative duties and was openly targeted by Lysenko.

On August 6, 1940, while he was on a collecting trip in the western Ukraine, Vavilov was arrested by Soviet agents. He was subsequently found guilty of trumped-up charges, including conducting sabotage on Soviet agriculture on behalf of Western powers. He was sentenced to death, but through the efforts of his brother, Sergey, he was instead imprisoned for ten years. He died while in prison on January 16, 1943, as a result of malnutrition.

Vavilov's case was examined closely after Stalin's death. He was subsequently rehabilitated, his scientific work was republished, and his contributions fully noted. He remains one of the most tragic figures in the history of science and his plight serves as a grim lesson against the ideological control of science. SEE ALSO AGRICULTURE, HISTORY OF; BIOGEOGRAPHY; BREEDING; CANDOLLE, AUGUSTIN DE; EVOLUTION OF PLANTS, HISTORY OF; FABACEAE.

Vassiliki Betty Smocovitis

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Vegetables

The term *vegetables* can have three distinct meanings when applied to plants. The first as in "animal, vegetable, or mineral" refers to the entire kingdom of green plants: algae, mosses, ferns, and flowering plants, and maybe including nongreen fungi and bacteria. The botanical sense of vegetables refers to all plant parts such as roots, stems, and leaves excluding the reproductive structures of flowers, fruits, and seeds, so that there is a vegetative phase of plant growth and a reproductive phase that is quite distinct. The third usage and the one most commonly understood refers to plant structures that are predominately water, edible without much woody fiber (cellulose), easily eaten raw, and low in sugar. This "kitchen sense" of the word vegetable as in "eat your vegetables" refers to botanical vegetables such as roots (e.g., radishes, parsnips, and carrots), underground stems or tubers (e.g., potatoes), young stems (e.g., asparagus and bamboo shoots), short stems with surrounding fleshy leaves (e.g., onions), leaf stalks (e.g., celery and rhubarb), leaves (e.g., lettuce and parsley), buds (e.g., cabbage and palm hearts), and extends into reproductive structures such as unopened flowers (e.g., broccoli and artichokes), fruit (e.g., tomatoes, okra, bell peppers, green beans, eggplants, and cucumbers), and seeds (e.g., green peas). "Kitchen-sense" vegetables are generally excellent sources of vitamins A and C, as well as

The common bean plant (*Phaseolus vulgaris*).

minerals, while being low in overall calories. Mushrooms are also considered vegetables in this sense. They are the reproductive structure of fungi.

Vegetables are consistently high in water and eaten when young and immature before much plant fiber has developed. Many vegetables are biennials, which grow the first year and accumulate materials in the root or other vegetative part to use in flowering the second year. Examples are carrots, beets, parsnips, and rutabaga, which are harvested the first year before the root turns woody. Many fruits are eaten immature before the enclosed seeds develop fully, such as zucchini, crookneck squash, sweet corn, snow pea, and chayote. Some vegetables are 91 to 95 percent water (cabbage, tomato, spinach), others are 85 to 95 percent water (carrots, artichoke, brussels sprouts) and some are 70 to 80 percent water (sweet corn, peas, sweet potato, parsnips, potato). The later are high in starch. The high water content explains why most vegetables are low in calories.

The most-consumed vegetable across cultures is the tomato, much of it being processed for sauces and other tomato-based products. Originally from Mexico, this fruit, which is used as a vegetable, has been adopted by almost every cooking style. The onion and its various pungent lily relatives are the vegetables with the highest sugar content and are found in cooking (which brings out the sugar) worldwide. The vegetable with the most forms from a single species, *Brassica oleraceo*, are the Mediterranean cabbage relatives: kale, collards, broccoli, and cauliflower known from Greek and Roman times, headed cabbage from the Middle Ages to brussels sprouts and kholrabi from the time of the **Renaissance**. The potato is the world's number-one vegetable by tonnage harvested but is seldom eaten raw and is more often classified as a starchy tuber. SEE ALSO Economic Importance of Plants; Fruits; Potato.

Renaissance a period of artistic and intellectual expansion in Europe from the fourteenth to the sixteenth century

Garrison Wilkes

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W

Warming, Johannes

Danish Botanist
1841–1924

Johannes Warming was a Danish botanist who is regarded as the founder of plant ecology. The term ecology had been used before, but Warming was the first to describe the fundamental questions that must be addressed in a study of plant ecology and the first to popularize detailed research into the ways plants relate to their environments.

Warming was born November 3, 1841, in Mandø, Denmark. His father was a Lutheran minister there on one of the northern Frisian Islands. Warming loved living there on the coast and he later wrote about his homeland's marshlands and dunes. From his early observations there, he compiled written records that are still important for the study of the ecology of the area's plants today.

Early Research on Structure and Adaption

In his early twenties, while he was a student, Warming became the secretary for a Danish zoologist, P. W. Lund, who was studying fossils in Brazil. Warming accompanied him to Minas Gerais, Brazil, and he spent three years there from 1863 until 1866. While there, Warming carefully studied the environment in that tropical savanna climate. He compiled writings and observations that would be the most thorough examination of a tropical environment at that time. It took Warming nearly twenty-five years to complete the organization and publication of his descriptions of the Brazilian environment. His outstanding work was a detailed record of the plants there; it carefully explained the range of plant geography in the area. At that time, before the study of plant ecology as Warming later introduced it, plant geographers were only beginning to document the regional differences between plants and the effects the surrounding environment might have on plants. Warming then studied plant geography, but he would soon begin the study of plant ecology.

Warming left Brazil to study with respected botanists, first in Munich and then in Bonn, Germany, in 1871. At this time he began detailed research into plant **morphology**, which was then a popular branch of botany. In studying morphology, he made observations about the functions and origins of different plant structures, particularly floral structures. His work was important to the understanding of the development of the stamen and the ovule, and to research into the general morphology of the flower. He did interesting work with carnivorous plants such as *Drosera*, which catches insects in its many sticky tentacles. Warming carefully observed these tentacles, trying to determine the mechanism of their movement.

morphology shape and form

In the late 1870s, Warming became interested in evolution, as had recently been described by Darwin and Lamarck. Warming became a dedicated proponent of the Lamarckian ideas about the causes of evolution. With these ideas in mind, Warming published several more papers about the structure and morphology of different plants and flowers. He classified these plants morphologically and paid special attention to the features of these plants that might help them adapt to their environment. Most of the plants he described were Scandinavian, and he was able to present them in a very clear and easily understood way in his texts. In these early studies, Warming had proved himself to be a careful and thoughtful botanist, and in 1886 he became a professor of botany at the University of Copenhagen. He stayed working there for twenty-five years, until 1911.

Foundations of Plant Community Ecology

Warming went on to develop his interest in plant adaptations, and it led to the publication in 1895 of his work *Ecology of Plants* or *Plantesamfund*, as it was originally published. This work was the first plant ecology text and it laid the foundations for the new ecological branch of botanical research, inspiring many botanists to study plant ecology. In it, Warming described his ideas about the types of questions one should ask when examining **populations** of plants. He wanted to know why each plant had a particular habitat, why different plant species would often occur in communities, and why these communities would have specific characteristic growth patterns. The book was sensational among botanists at the time. It proposed a new way to group and describe associations between plants. Warming's ideas about

population a group of organisms of a single species that exist in the same region and interbreed

plant communities had come out of his study of plant geography and the idea of a community of plants was a new term in botany and plant geography. It applied to a group of different species that interacted together to form a well-defined unit, such as a lake or meadow. Warming divided plant communities into four types. These types were based on whether the plants lived in wet, dry, salty, or moderate environments. Water figured closely in his descriptions, as Warming generally considered it to be the most important factor influencing plant communities.

His idea about communities of plants being influenced as units was a brilliant new way to look at plants in general. Warming suggested that botanists examine all the environmental factors that effect the growth of a plant. These factors would affect individual plants, but they would also affect others plants in the area. Together these influences would then affect the ways that the different plants interacted with each other in the community.

Among all his publications, *Plantesamfund* was probably the most important, as it started a whole new field of study. Warming's ability to discern the details of plants' relationships with their environments influenced all of his writings, but in his book on ecology it brought the desire of ecological research to many other botanists. In the following years, numerous ecology publications appeared. The next century saw the development and growth of the ecological movement, as people began to understand the interactions not just between plants, but between plants, their environments, and the animals (including humans) that encounter them. Warming had seen an explosion of ecological awareness begin by the time he died in Copenhagen on April 2, 1924, and he will be remembered as the founding pioneer of ecological research. SEE ALSO ECOLOGY; ECOLOGY, HISTORY OF; PLANT COMMUNITY PROCESSES; ODUM, EUGENE.

Jessica P. Penney

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Water Movement

Plants that grow on land (terrestrial plants) find the materials they require for life in two different locations. The soil is the source of water and minerals to be used for a variety of functions, while the atmosphere provides carbon dioxide for photosynthesis. The root system takes up water and minerals from the soil, while the shoot system, consisting of leaves and stems, carries out photosynthesis. As larger plants evolved, the roots and shoots became increasingly distant from each other, and long-distance transport systems (xylem and phloem) became necessary for survival. Clearly, one of the most important functions of the root system is the absorption of water.

How does the root absorb water? Once inside the plant, how do water and dissolved minerals move from the root to the shoot? What happens to the water once it is delivered to the leaves by the xylem? To answer these questions, it is useful to discuss the end of the transport process first, since it is there that the driving force is found.

Transpiration

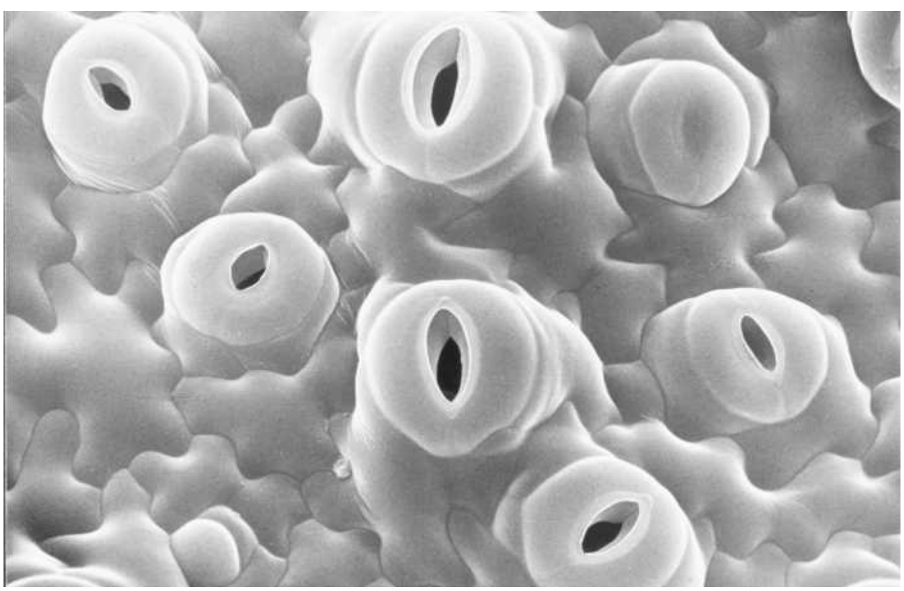
Nearly 99 percent of the water taken up by plants is lost to the atmosphere through small pores located mainly on the lower surface of leaves. Estimates of water loss by a single corn plant exceed 200 liters (53 gallons) over a growing season. This loss of water by the shoots of plants is called transpiration. Transpiration provides the driving force for the movement of water up the plant from the roots to the leaves. This movement ultimately results in further uptake of water from the soil.

Of course, the water taken up by the plant serves functions within the plant as well. Water is the environment in which life and its reactions occur. Water, and the materials dissolved or suspended in it, make up the cytoplasm of cells and the interior of cellular compartments. It is the uptake of water that drives the growth of plant cells. Water enters into many reactions or chemical changes in cells, including the reactions that capture light energy during photosynthesis.

The Causes of Transpiration. The small pores through which shoots lose water to the atmosphere are called stomata. These pores, which allow carbon dioxide into the plant from the surrounding air, are actually spaces between the cells that make up the "skin," or epidermis, of the shoot. Stomata can be open or closed, depending on the action of a pair of cells, called guard cells, surrounding the pore.

Stomata open in response to the plant's requirement for carbon dioxide in photosynthesis. The carbon dioxide cannot move directly into the shoot cells because the outside of the shoot is covered with an impenetrable waxy coating, the **cuticle**. This coating prevents the plant from drying

cuticle the waxy outer coating of a leaf or other structure, providing protection against predators, infection, and water loss



Scanning electron micrograph of the stomata on the surface of a tobacco leaf.

out but also prevents the movement of carbon dioxide into the leaves. The presence of the stomata allows for sufficient carbon dioxide to reach the leaf cells mainly responsible for photosynthesis.

Not only does carbon dioxide move into the plant when the stomata are open, but water in the form of water vapor also moves out of the plant, driven by the difference in water concentration between the plant and the atmosphere. The opening and closing of the stomatal pores maximize the uptake of carbon dioxide and minimize the loss of water by the shoot. Thus, two of the major signals that cause the stomata to open are the absorption of light and the low concentration of carbon dioxide in the leaves. As a result of these signals, most plants open their stomata during the day, when light energy is available for photosynthesis, and close them at night. Water stress, that is, a water deficit sufficient to prevent normal functioning, can override these signals and cause the pores to close in order to prevent excess water loss. For a plant, taking up carbon dioxide for growth is secondary when further water loss might threaten survival.

While transpiration is often described as a necessary evil, it does serve to cool leaves under conditions of high light absorption. The evaporation of water from leaves thus serves the same purpose for plants as sweating does for humans. Transpiration also speeds up the flow of water and dissolved minerals from the roots to the shoots. In the absence of transpiration, however, other mechanisms would cool the leaves, and water would continue to flow, though at a much lower rate, as it was used in the leaves.

The Nature of Transpiration. Transpiration is an example of diffusion, the net movement of a substance from a region of high concentration to a region of lower concentration. Diffusion accounts for transpiration because the air inside the plant is very moist, while the atmosphere surrounding the plant almost always contains less water vapor than the inside of the plant. The relative humidity of the air inside a leaf usually ranges from 98 to 100 percent, while the atmosphere rarely approaches such high values. (Relative humidity [RH] is the amount of water in the air compared to the maximum amount that could be held at that temperature.) These differences in relative humidity reflect differences in water vapor concentration, the driving force for diffusion. For example, assume that both the leaf and the atmosphere are at the same temperature of 20°C (68°F) and that the atmosphere is at a relative humidity of 50 percent. Then the air inside the leaf holds 10.9 grams of water per cubic meter, and the atmosphere holds only 5.5 grams of water per cubic meter. If the leaf is warmer than the atmosphere, a common occurrence, the difference in water vapor concentration will be even higher.

The Transpiration-Cohesion-Tension Mechanism for the Transport of Water in the Xylem

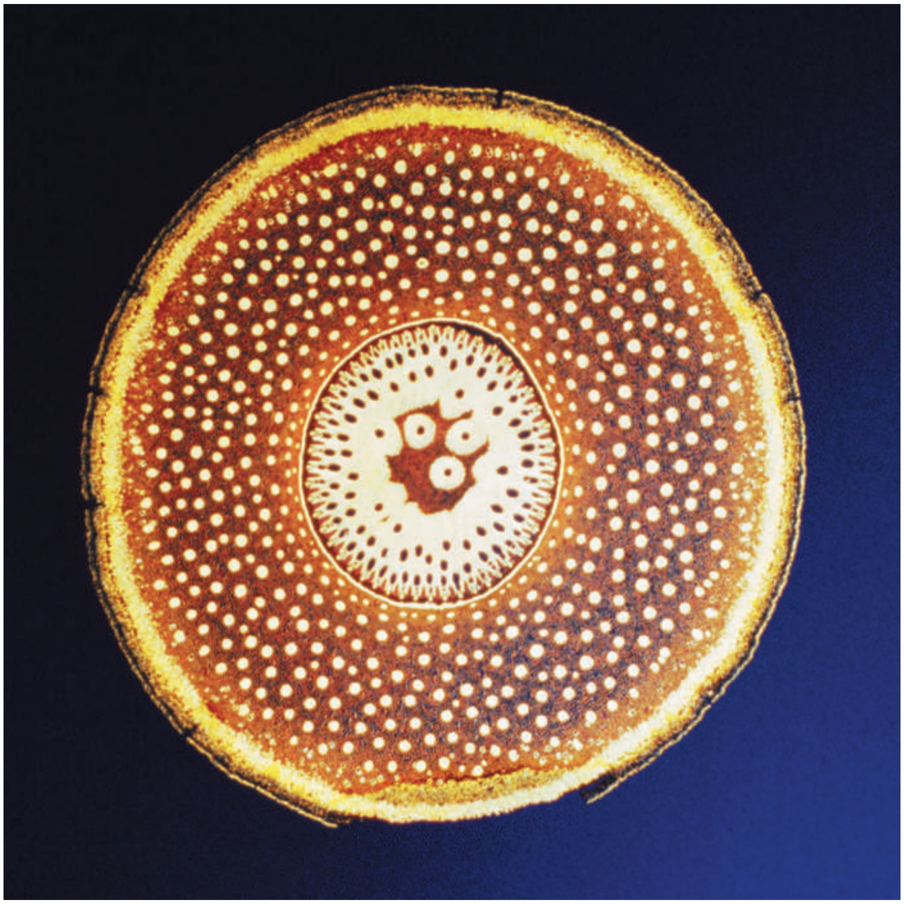
The problem of how water moves upward in plants from roots to shoots is most extreme in the tallest trees, where distances to be traveled are the greatest. Some of the tallest trees are at least 120 meters (394 feet) tall. If a hypothesis or model can explain water movement in these tallest plants, then the model can also explain it in smaller examples. Much of the research on the mechanism of water transport has been performed on relatively tall trees.

Since around the 1960s one mechanism has been the most widely accepted explanation for how water moves in the xylem. This mechanism is intimately connected to the process of transpiration described above.

Xylem Transport Cells. The xylem has a number of kinds of cells and so is called a complex tissue. The xylem vessels are the cells that actually transport water and dissolved minerals from the root. Two types of xylem vessels exist: vessel members and tracheids.

While vessel members and tracheids differ in a number of respects, they share one prominent structural feature: both are dead when transporting water. For xylem vessels, the production of strong secondary walls and the death of the cell are key characteristics that must be taken into account by any proposed mechanism. Also significant is the fact that cell walls are permeable to the flow of water, though they do offer some resistance to the flow.

Inadequate Explanations for the Movement of Water from Roots to Shoots. Ideas to explain the uptake and transport of water are of two basic types. Either water can be pushed (pumped) from the bottom of the plant, or it can be pulled to the top. Early experimenters attempted to explain water movement in terms of pumps, which were thought to be located either in the roots or all along the path of water movement. Pumping water requires energy, and only the living cells in the plant expend energy. So, in 1893 a German researcher named Eduard Strasburger tested the hypothesis that living cells in the plant push water up the stem. He cut twenty-



Cross-section micrograph of a root of a species of *Pandanus* conifer showing xylem, phloem, and cortex cells.

meter-tall trees off at the base and placed the cut stumps in buckets of poisons that would kill any living cells that were contacted. The trees continued to transport water despite the death of the living cells in the trunks. This experiment demonstrated that living stem cells are not required for transport of water through the stem. Further, the experiment showed that the roots are not necessary for the transport of water.

One “pull” model for water transport in the xylem is capillarity, the rise of some liquids in small tubes that are made of materials to which the liquid is attracted. However, capillarity can only pull water to a height of less than half a meter (ten and a half feet) in tubes the size of xylem vessels. This mechanism is clearly inadequate to explain water transport in tall trees.

The Transpiration-Cohesion-Tension Mechanism

An alternative pull model, the transpiration-cohesion-tension mechanism, is accepted as the best explanation thus far for water movement. The hypothesis has several components, as the name implies. Transpiration, the loss of water by the above-ground or aerial parts of the plant, has already been described. Cohesion refers to an attraction between molecules that are alike, in this case, water molecules. When water molecules interact, they are attracted to each other, the partial negative charge on the oxygen of one molecule being attracted to the partial positively charged hydrogen of another. These attractions, called hydrogen bonds, are quite important in the transpiration-cohesion mechanism.

Another important but less familiar idea is tension, or negative pressure. When a substance is compressed, a positive pressure higher than atmospheric pressure is generated. When a substance is being pulled from both ends, rather than compressed, a negative pressure, or tension, results that is lower than atmospheric pressure. One way to visualize a tension is to think about liquid in a syringe, which has the needle end sealed. When the plunger is pulled toward the back of the barrel, the liquid is pulled and is under a tension.

The transpiration-cohesion-tension mechanism can be explained as a series of sequential steps:

1. The first step is the diffusion of water from the leaf through the stomatal pores. This is transpiration, and it provides the force driving the transport of water.
2. As water exits the leaf, more water evaporates from the cell walls of the leaf into the extensive air spaces within the leaf.
3. As water evaporates from the cell walls, this loss pulls more liquid water from the xylem of the leaf. This flow occurs because the water in the tiny pores and crevices in the cell walls is continuous with the water in the xylem vessels and because the continuous water molecules are held together by the high cohesion of water.
4. Cohesion also accounts for the flow of the column of water from the xylem of the root to the xylem of the leaves, as water is lost through the stomata.
5. As water flows upward in the root, water influx from the soil fills the void.

The flow of water and dissolved minerals in the xylem is an example of bulk flow, the movement of a solution as a whole rather than as individual molecules. A more common example of bulk flow is the streaming of water with its dissolved minerals in the pipes of a house. One difference between the house and xylem examples is that the pressures in plumbing are positive pressures, and water is pushed out the faucet. The pressures in the xylem are negative pressures, and water is pulled up the plant. In both cases transport occurs from a region of higher pressure to lower pressure. The transport cells in the xylem are also unlike the living cells of the plant, which have positive pressures on the order of five to ten times atmospheric pressure.

Evidence for the Transpiration-Cohesion-Tension Mechanism. According to the transpiration-cohesion-tension mechanism, the process of water transport in the xylem is purely physical, with no energy input from living cells of the plant. This is consistent with the structure of the xylem vessels, which are nonliving. The cell walls of the xylem vessels are strong secondary walls, which can withstand the very negative pressures in the xylem stream. In order to pull water to the top of the tallest trees, the tensions at the top must be around negative thirty atmospheres.

Experimental evidence supports the transpiration-cohesion-tension mechanism as well. If the pressures in the xylem were positive and higher than atmospheric pressure, cutting through a xylem vessel would open the cut end to atmospheric pressure, and water would exude from the cut end. Since the pressures in the xylem are negative and lower than atmospheric, air is actually sucked into the cut end when the xylem vessels are cut, and water retreats into the xylem vessels. (Recutting cut flowers under water is good advice, since this refills the xylem vessels with water and keeps the flowers fresh longer.)

The retreat into the xylem vessels allows the tensions in the xylem to be measured by a device called a pressure bomb or pressure chamber. A leaf or twig is cut from the plant, and the blade is sealed into a strong metal chamber with the leaf stalk (petiole) or stem extending into the air. The chamber is pressurized until the contents of the xylem are forced back to their original position at the cut surface. The positive pressure required to restore the water to its original position is equal to, but opposite in sign, to the tension that existed in the xylem before it was cut. Tensions measured in the xylem higher up a tree are more negative than lower in the tree, in keeping with the proposed mechanism.

Questions About the Mechanism. The main controversy surrounding transpiration-cohesion-tension mechanism questions whether water columns in the xylem can withstand the tensions required for transport. In a large pipe a column of water can withstand very little tension before the column breaks and an air bubble forms. Bubble formation (cavitation) stops the flow of water in a xylem vessel in much the same way that vapor lock stops the flow of gasoline in the fuel line of a car. However, the tension that a liquid can sustain increases as the diameter of the vessel decreases, and xylem vessels are very small (twenty to several hundred micrometers in trees, for example), and as a result the tension they can sustain without cavitation is very high.

HENRY DIXON

Henry Dixon, an early researcher important in developing the cohesion theory, actually devised the pressure chamber in 1914, but made his chambers out of glass, with explosive results. Per Scholander first successfully used the pressure chamber in 1965 to measure the xylem tensions in tall Douglas-fir trees. He obtained his twig samples with the help of a sharpshooter who shot them down with a rifle.

Even so, bubbles do form in the xylem under various conditions such as drought, when very negative tensions are required to transport water. Using sensitive microphones, researchers can detect individual cavitation events as clicks that occur when the water column breaks. Although bubbles do form, water can move around a blocked xylem vessel, and plants can restore the continuity of the water columns in various ways. Researchers continue to investigate and question the cohesion mechanism, particularly new methods to measure tensions in the xylem.

Uptake of Water by Roots and the Movement of Water Into the Xylem

The mechanism for water uptake into roots differs from that for transpiration (diffusion) and for the flow of sap in the xylem (bulk flow). In order for water and dissolved minerals from the soil to enter the xylem of the root, cell membranes must be crossed. Osmosis is the movement of water across membranes that allow water to move freely but that control the movement of dissolved substances, such as mineral ions.

parenchyma one of three types of cells in ground tissue

ions charged particles

Why must water cross living cells as it moves across the root? Why can't water simply flow around the cells in the cell walls and enter the root xylem directly? The primary roots of plants generally consist of three concentric rings of tissue. On the outside is the epidermis, a single layer of cells usually lacking a thick waxy coating, suiting the root well for its role in water absorption. Next toward the center are layers of **parenchyma** cells that make up the cortex of the root. At the center of the root is the vascular tissue, including the xylem. The innermost layer of the cortex, the endodermis or "inner skin," has a special feature that prevents water movement through the cell walls of this layer. The walls that are perpendicular to the surface of the root contain waxy deposits called Casparian strips. The Casparian strips are impermeable to water and dissolved substances like mineral **ions** and thus block transport in the cell walls at the endodermis. Both water and minerals must enter the cytoplasm of the endodermal cells by crossing cell membranes. The water and minerals then cross into the vascular tissue by moving through living cells and cytoplasmic connections between them, finally exiting into the xylem by crossing yet another membrane.

The role of the Casparian strips is probably related more to the movement of mineral ions into the plant than to the movement of water. Mineral ions must cross membranes by means of special proteins in the membrane. Sometimes these proteins concentrate ions and other substances inside the cells by using cellular energy. By forcing mineral ions to cross membranes, the Casparian strips allow the plant to control which minerals will enter and to accumulate these ions to levels higher than in the soil water. SEE ALSO Anatomy of Plants; Cells, Specialized Types; Leaves; Photosynthesis, Carbon Fixation and; Photosynthesis, Light Reactions and; Roots; Stems; Vascular Tissues.

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Weeds

Weeds represent the most important pest complex affecting humans throughout the world. In the United States, weeds are estimated to cost the economy more than $20 billion annually. Weeds negatively affect food and fiber production, human and animal health, and the quality of life for the world population. For instance, weeds impact humankind by causing crop failures, triggering allergic reactions, and reducing the esthetic quality of lawns. Interestingly, of the thousands of plant species in the world, less than 250, or approximately one-tenth of a percent, are considered important weeds.

There are a number of definitions for weeds. The Weed Science Society of America in 1994 defined weeds simply as "plants that are objectionable or interfere with the activities or welfare of man." However, an ecological definition describing the characteristics that allow some plants to be weeds is more useful. These characteristics include: the ability to establish in disturbed habitats; the ability to grow and reproduce across a wide range of climatic conditions; seed dormancy; nonspecific germination requirements; rapid growth; high seed production; and unspecialized pollination. Weeds can improve their success by releasing metabolic **compounds** that interfere with neighboring plants. These compounds are allelotoxins, and the resulting allelopathic response on other plants may represent a future weed management opportunity.

compound a substance formed from two or more elements

Weeds growing in a North Dakota wheat stubble field.

The importance of weeds has resulted in a significant number of herbicides applied worldwide. Further, tillage (soil disturbance) is also a primary tactic used to manage weeds. These strategies may result in soil erosion and herbicides leaching to ground water. However, the benefits of the judicious use of these tactics has resulted in dramatically higher food production and increased agricultural efficiency. Biological control tactics such as using insects or diseases to attack weeds have not been effective in most annual food crops but may hold promise for the future. SEE ALSO Allelopathy; Herbicides; Interactions, Plant-Plant; Invasive Species; Kudzu.

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Wetlands

Wetlands are habitats characterized by saturated (waterlogged) soils for at least part of the year and plants that are adapted to grow under wet conditions. They may be completely covered by water or the water may be just below the ground. There are many different types of wetlands, such as swamps (wetlands dominated by trees), marshes (wetlands dominated by nonwoody plants such as grasses and sedges), wet meadows, bogs, fens, floodplain forests, lakes, and ponds.

water table level of water in the soil

Wetlands are to a large extent the product of the topography of the land. They develop wherever there is a depression in the land that brings the **water table** (groundwater) close to or even above ground. The type of wetland that will develop in a particular area depends on the rate of water flow, the length of the season of soil saturation, latitude (polar versus temperate versus tropical), proximity to the coast (marine versus freshwater wetlands), and the surrounding geology.

Plant Adaptations to Wetlands

stomata openings between guard cells on the underside of leaves that allow gas exchange

It is challenging for a plants to grow in constantly damp conditions. The saturated soil contains little or no oxygen compared to upland soil, therefore the roots of wetland plants require special adaptations to enable them to survive. Water lilies have air channels that run from their leaves, which are in constant contact with the air, to their roots under water. Water lilies also have their **stomata** only on the upper surface of their leaves (most plants have stomata on the lower surface) so that water can not enter when these pores open to allow carbon dioxide in for photosynthesis. Salt marsh grasses (*Spartina* species) also transport oxygen to their roots, where it may be excreted into the surrounding soil and create a small oxygenated zone around their roots. Plants that grow completely underwater, such as seagrasses and pondweeds, use the oxygen created as a by-product of photosynthesis to aerate their roots. Most wetland plants have also adapted to wet conditions through changes in their metabolism. Non-wetland plants, for example, typically produce an alcohol (ethanol) as a breakdown product of sugar me-

Wetlands develop wherever there is a depression in the land that brings the water table close to or even above ground.

tabolism when the soil is saturated with water. Ethanol is toxic to plants. Wetland plants have different **enzymes** that prevent the formation of the alcohol.

enzyme a protein that controls a reaction in a cell

Although only a limited number of species can thrive in the constantly saturated soils of wetlands, those plants that have adapted are often extremely productive. As anyone who has planted a garden knows, one of the major factors limiting the growth of terrestrial plants is water. Having adapted to life in constantly damp conditions, wetland plants never have to worry about getting water. As a result, their growth rates can be very high.

The Value of Wetlands to Humans

Wetlands are very important features in the landscape and provide humans with some tangible benefits. They act like a sponge helping to reduce the impacts of floods by absorbing water and serving as a reservoir for groundwater. As water flows through a wetland, pollutants such as excess silt and harmful nutrients are trapped; thus, the wetland acts as a filter of pollutants and helps to maintain clean water. Wetlands serve as a vital habitat to many different species of wildlife, including many that are very rare and in danger of extinction.

The value of wetlands has not always been appreciated. A conservative estimate is that over 30 percent of the original wetlands in the United States have been lost forever. These were filled in the past to make way for farms, houses, highways, businesses, and other human activity. Since the early 1970s, the attitude toward wetlands has changed. Not only are there now strong efforts in most states to protect the remaining wetlands, many environmental agencies and land conservation groups are working to restore wetlands damaged by past human activities.

Current Threats to Wetlands

Even with a greater sense of the value of wetlands among much of the public, there are still pressures on these habitats. The ability of wetlands to

GROWTH HABITS OF WETLAND PLANTS

Growth Habit	Examples
Completely submerged	Sea grasses, pondweeds, water plantain, water milfoil, elodea
Floating plants, unrooted in substrate	Duckweeds, bladderworts, water hyacinth
Floating leaves, rooted in substrate	Water lilies, lotus, floating hearts, water chestnut
Emergent perennials: roots in substrate under water, leaves and stems above water	Cattails, common reed, purple loosestrife, salt marsh grasses, tule, saw grass, wild rice
Emergent shrubs	Buttonbush, alders, leather leaf, sweet gale
Trees: constantly submerged	Mangroves, bald cypress, black spruce
Trees of floodplains: tolerate periodic flooding	Cottonwood, willow, silver maple, black ash

absorb pollutants is not unlimited. Excessive amounts of pollution entering a wetland over a long period of time is likely to cause long-term changes in the wetland. One of the world's most famous wetlands, the Everglades of southern Florida, has suffered for years from pollution from fertilizers used by farms upstream from it. The pollution has resulted in some major changes in the plant **community** and suspected declines in the diversity of animals it supports.

community a group of organisms of different species living in a region

Another major threat to wetlands is changes in hydrology (the flow of water). Water is the lifeblood of wetlands. If too much water is removed for human consumption or to irrigate cropland, the wetland may be degraded into a less-valuable habitat or even disappear completely. The Florida Everglades has to compete with the farms and rapidly growing cities of southern Florida for this precious resource and has suffered as a result. Not only is the quantity of water important to maintaining wetlands, but so is the timing. Many wetlands depend on seasonal flooding followed by a dry period. This type of natural cycle may be altered by dams, which may hold back the water during the wet season.

Direct filling of wetlands, although less common than it was twenty years ago, still occurs, particularly with smaller wetlands that may be perceived as less valuable than larger ones. Some small wetland types contain rare species of animals precisely because they are too small and temporary in existence to support fish predators, pointing out that size is not always a good indicator of value.

Finally, many wetlands throughout the world are threatened by invasions of nonnative plant species. Purple loosestrife, a European garden plant, has taken over many freshwater marshes in the northeastern United States. West Coast salt marshes are threatened with being overrun by tall cordgrass, an East Coast salt marsh species. These are only two examples of a very widespread problem. SEE ALSO Aquatic Ecosystems; Aquatic Plants; Carnivorous Plants; Endangered Plants; Invasive Species; Peat Bogs.

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Wheat

Common wheat (*Triticum aestivum*) is an annual cool season grass that is grown across a wide range of environments around the world. It has the broadest range of adaptation of all the cereals and more land is devoted to wheat than any other commercial crop. Wheat is the number-one food grain consumed directly by humans, and its production leads all crops, including rice, maize, and potatoes.

Wheat is a typical grass in that it forms several leafy shoots that grow about one meter in height. Each shoot has five to seven nodes and produces an **inflorescence** that is a thick condensed spike. Each spike has a main axis bearing spikelets separated by short internodes with two to five florets within each spikelet. Wheat normally has thirty to forty kernels per spike and is self-pollinated. The moisture content of the seed is about 10 percent, which makes wheat grain easy to store and transport.

inflorescence an arrangement of flowers on a stalk

This crop is the most important source of carbohydrates in the majority of countries in the temperate zone. Wheat is an excellent food, even though the grain is deficient in some essential amino acids (it is particularly low in lysine). Wheat starch is easily digested, as is most wheat protein. The grain contains minerals, vitamins, and fats (lipids), and when wheat products are complemented by small amounts of animal or **legume** protein, the combination is highly nutritious. A predominantly wheat-based diet is higher in fiber and lower in fats than a meat-based diet.

legumes beans and other members of the Fabaceae family

Most of the wheat marketed is used to manufacture flour from which bread, cakes, cookies, crackers, and pastries are made. Wheat grain is an excellent livestock feed, as are many of the by-products from the milling of the grain into flour. Normally about 70 percent of the grain can be made into flour and the rest into very useful by-products. Also, the green plants can be used for livestock forage.

Wheat has unique baking properties, the most important of which is the elasticity of its gluten protein. The amount and quality of the gluten pro-

More land is devoted to wheat than to any other commercial crop.

duced by any particular type are prime factors in determining the quality of the flour that can be obtained from the milling process. Unlike any other grain or plant product, wheat gluten enables dough to rise through the formation of small gas cells that retain the carbon dioxide formed during yeast fermentation or chemical leavening. This is what gives bread its porous structure. Bread has been a basic food for humans throughout recorded history, and probably for a much longer period: it remains the principal food product made from wheat.

Wheat is divided into several classes based on the level of the gluten protein. Hard wheats are high in protein (13 to 15 percent) with strong gluten strength and are used primarily for bread making. Soft wheats are low in protein (10 to 12 percent) with weak gluten strength and are used for cakes, cookies, and other pastries.

There are also two types of wheat based on the season they are grown. Winter wheat is fall planted and is harvested in early summer. Spring wheat is planted in the early spring and harvested in the summer. Winter wheat is quite winter hardy and actually requires cold temperatures in order to head out and produce a grain crop, whereas spring wheat is not winter hardy and does not have a cold requirement to produce grain.

A crop of wheat is harvested somewhere in the world during every month of the year. Most of the global harvest, however, occurs between April and September in the temperate zone of the Northern Hemisphere; considerably less wheat is grown in the Southern Hemisphere, where harvest occurs from October to January.

The culture of wheat is highly mechanized with large grain drills used to plant and large combines to harvest. A single person can grow hundreds of acres since it is not labor intensive. Wheat does not require as much fertilizer as most other crops and only occasionally requires pesticides such as fungicides, herbicides, or insecticides. Wheat is less profitable on a per-acre basis than many other crops and to date no genetically transformed wheat has been grown on a commercial scale. A great deal of research is being done with wheat and it is probable that genetically engineered wheat will be available in the near future. SEE ALSO Agriculture, History of; Agriculture, Modern; Economic Importance of Plants; Grains; Transgenic Plants.

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Wood Anatomy

Woody trees such as the giant sequoia of California and the blue gum of Australia are among the world's largest organisms. Despite the tremendous bulk of their stems, only a relatively thin layer of tissue between the bark and the wood is actually alive and continues to produce new layers of wood throughout the life of the tree. How the **meristematic** tissue that produces these layers remains active for hundreds or even thousands of years is one of the major unanswered questions of plant biology.

meristematic related to cell division at the tip

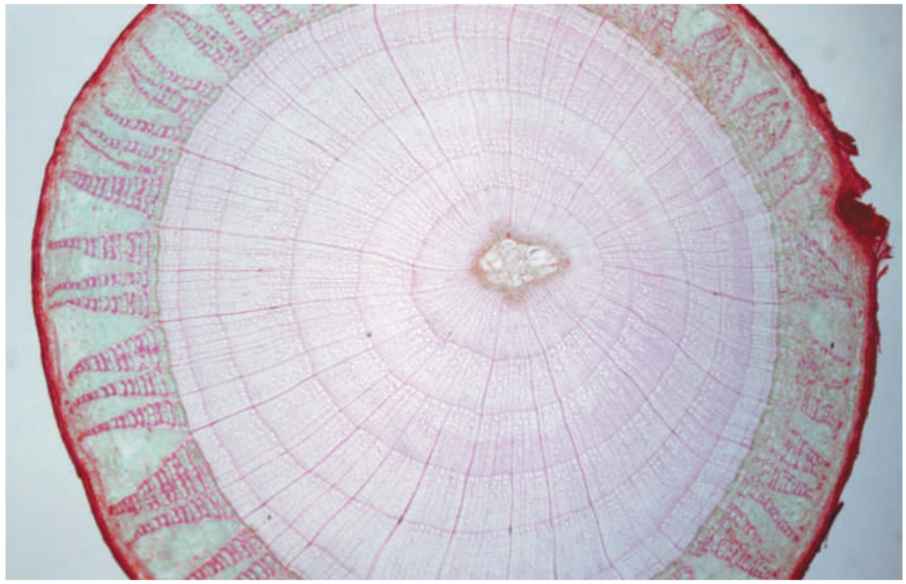
Meristematic Regions and Growth Patterns of Woody Plants

Plant embryos inside the seed are tiny rudimentary individuals that have the potential to produce the entire adult plant. This potential for growth rests in specialized areas of the embryo called the **apical meristems**. Upon seed germination, the root apical meristem at the basal end of the embryo starts to grow and to produce the root system of the plant. The shoot apical meristem at the opposite end of the embryo produces the shoot system. These apical meristems extend the length of the stem-root axis and, through cell proliferation, produce all the primary tissues of the plant body (epidermis, vascular tissues, and ground tissues). Plants belonging to the monocot group have only apical meristems. While some monocot stems become thick through primary thickening growth and become large trees like the date palm, monocots are never truly woody plants because they lack a vascular cambium.

apical meristem region of dividing cells at the tips of growing plants

In contrast, almost all plants belonging to the dicot group have two types of lateral meristems that increase the girth of the stems and roots: vascular cambium and cork cambium. The vascular cambium arises within the tissues of the stem and root. It first appears between the xylem and phloem of the vascular bundles and then extends between the vascular bundles to form a continuous sheet of cells around the stem. The defining feature of the vascular cambium is its distinctive plane of cell division: vascular cambium cells called cambial initials divide periclinally (that is, in a plane that is parallel with the surface of the stem and root). Cells derived from divisions of the cambial initials are called derivatives. Derivatives formed toward the inside of the stem and root become xylem cells, while derivatives formed toward the outside become phloem cells. The tissues formed by a lateral meristem are called secondary tissues, so the vascular cambium produces secondary xylem (wood) and secondary phloem.

The cells of secondary xylem tissue have hard, rigid cell walls and do not compress easily. Therefore, as the cambial initials produce increasingly more secondary xylem derivatives and the stem or root increase in girth, the cambium and all other tissues to the exterior begin to be stretched. This is often the signal for the formation of the second kind of lateral meristem, the cork cambium. In the stem, the cork cambium usually arises just under the epidermis, while in the root the cork cambium arises closer to the vascular tissue, from the pericycle. In each case, the initials of the cork cambium divide periclinally, like the vascular cambium, but the cork cambium produces derivative cells only toward the outside. These derivatives mature as cork tissue, a compact, waterproof, and airtight layer that protects internal cells.



A magnified transverse section of a piece of wood reveals its growth rings.

Many common wild and garden plants such as roses, sunflowers, and asters have both vascular and cork cambiums that produce secondary vascular and cork tissues. These plants live for a relatively short time and their lateral meristems produce only a moderate amount of secondary tissue. Other plants live for decades or centuries, and their lateral meristems produce secondary tissues year after year, building up massive volumes of wood and bark. These are the true woody plants, and most produce a large main stem or trunk, with smaller lateral branches.

Anatomy of a Woody Stem

Many features of wood and bark can be identified in a tree stump without a microscope's magnification. Growth rings reflect the annual activity of the vascular cambium. Early in the growing season, the cambium produces xylem derivatives that mature as wide, thin-walled cells, forming a visible light layer of wood called the earlywood. Later in the growing season, xylem derivatives mature as narrower, thicker-walled cells, forming a darker layer in the wood called latewood. In temperate climates, each pair of earlywood and latewood layers form a recognizable annual ring. In years when conditions for tree growth are good, the vascular cambium divides actively and produces a wide annual ring. When growth conditions are poor, the cambium divides slowly, and the annual ring is narrow. The distinctive pattern of wide and narrow annual rings in a tree trunk provides clues about tree growth rates in the past, often for periods that extend for hundreds of years. **Dendrochronologists** use this information to make deductions about past climatic conditions and, in some cases, can determine the exact dates that a piece of wood from an ancient building was part of a living tree.

Many trees have a darker region of wood at the center of the trunk or root called heartwood. The coloration arises from **tannins** and other substances that retard decay created by xylem **parenchyma** cells before they die. Since the conducting cells (vessel elements and **tracheids**) and the sup-

dendrochronologist a scientist who uses tree rings to determine climate or other features of the past

tannins compounds produced by plants that usually serve protective functions; often colored and used for "tanning" and dyeing

parenchyma one of three types of plant cell

tracheid a type of xylem cell for water transport porting cells (sclerenchyma fibers) are already dead, the entire heartwood is nonliving. The lighter wood toward the outside of the trunk is called sapwood. Sapwood contains living parenchyma cells that function in storage and to recover nutrients from the sap. Although the entire sapwood region is moist, usually only the outer growth rings nearest the vascular cambium actually transport water from the roots to the leaves.

Another conspicuous feature of woody stems and roots are the panels of parenchyma tissue called rays that extend radially from the center of the heartwood, across the cambium, and into the bark. The ray parenchyma cells are produced by specialized cambium initials called ray initials and function as other xylem parenchyma cells. In some kinds of wood such as oak, the rays are very wide; in others such as pine, the rays are very narrow.

The bark found at the exterior of woody stems and roots is a composite structure. The secondary phloem that conducts the products of photosynthesis from leaves to roots is located directly adjacent to the vascular cambium. In most trees, the sieve elements of the secondary phloem are able to **translocate** for only one year. As the phloem ages, it becomes nonfunctional. Before all the phloem cells die, some of the parenchyma cells give rise to a new cork cambium that produces a new layer of cork tissue. Thus, bark is composed of alternating layers of dead phloem and cork tissues, with the only living cells found toward the inside. Thus woody stems have a thick insulating layer that protects the delicate vascular cambium within.

translocate to move, especially to move sugars from the leaf to other parts of the plant

Differences Between Hardwood and Softwood

Hardwood is the term used for the strong, dense wood of **angiosperm** trees such as maple, oak, and mahogany. Usually more than 50 percent of the volume of the wood is composed of sclerenchyma fibers, cells with extremely thick, lignin-impregnated walls, which give the wood its great physical strength. The remainder of the wood consists of conducting cells, the vessel elements and tracheids, and parenchyma cells. Hardwood trees vary in the arrangement of these cells within the annual ring. Some, like oak and elm, have wide, thin-walled vessel elements in the earlywood and much narrower vessel elements in the latewood, accentuating the differences between the two parts of the annual growth ring. This pattern is referred to as ring porous wood. Other hardwoods such as maple and willow have vessel elements of more uniform diameter scattered across the growth ring. This pattern is called diffuse porous wood.

angiosperm a flowering plant

The term softwood is used for the wood of conifers such as pines, firs, and spruces. The wood tends to be softer and less dense because it lacks the specialized sclerenchyma fibers of the hardwoods. Most of the volume of conifer wood is occupied by tracheids, cells that both conduct water and provide mechanical support. Because they carry out both functions, tracheids have relatively thin cell walls. The parenchyma tissue of softwoods often contains resin-filled ducts; these are part of the tree's defense system against insects and fungal diseases. SEE ALSO Anatomy of Plants; Conifers; Cork; Dendrochronology; Trees; Vascular Tissues; Wood Products.

Nancy G. Dengler

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Wood Products

artifacts pots, tools, or other cultural objects

Wood is one of the most significant structural materials used throughout human history. As documented by the earliest **artifacts** of human activity, wood has been associated with activities of hunting and gathering, early development of agriculture, and the foundations of civilization, as well as its obvious use as a fuel for fire. Archaeological studies of virtually every known civilization confirm the use of wood for a wide range of items and attest to wood's intimate involvement with human evolution and its progress through time.

As a structural material, wood has some rather remarkable properties. Despite its relatively low density (most woods float), it has physical characteristics that make it highly suitable for the building of structures that require resistance to bending, limited compressibility, relative ease of forming the members, and reliable means of attaching the structures together. In addition, properly prepared wood also possess aesthetic and physical beauty due to its color, strength, and grain characteristics that are highly valued in the fabrication of fine furniture and architectural components.

Dimensional Lumber

gymnosperm a major group of plants that includes the conifers

angiosperm a flowering plant

Among the many uses of wood products, the production of dimensional lumber ranks as one of the most significant, particularly in the construction of residential dwellings. The majority of timber species used for dimensional lumber are conifers (**gymnosperms**), which are typically evergreen (nondeciduous) trees, and come from areas where these plants are the major component of the flora in their habitats (e.g., coniferous forests). The wood produced from them is called softwood despite the fact that for many species it is quite hard and durable. This term is used in contrast to hardwood, a term applied to the wood obtained from **angiosperm** trees, which are typically (but not always) deciduous, and have slightly different cellular characteristics of their xylem. In North America, three major groups of conifers are used for the majority of dimensional lumber: spruce (*Picea* spp.), pine (*Pinus* spp.), and fir (*Abies* spp. or *Pseudotsuga* spp.). The woods of these species are very similar in appearance and have similar construction properties. The lumber industry identifies wood produced from them as SPF lumber (spruce–pine–fir), and this forms the bulk of the wood used for the construction of houses.

In the building trades, dimensional lumber is typically referred to as "2-by" material, alluding to the thickness dimension (in inches) of the rough lumber as it is sawn at a mill. A 2×4 when rough-sawn is nominally 2 inches (5 centimeters) in thickness by 4 inches (10 centimeters) in width and is supplied in standard lengths of 8, 10, 12, 14, 16, and 20 feet, depending on the

The wood frame of a new house being erected in Lone Pine, California.

length of the felled log before sawing. After drying the wood and surfacing the faces, a 2 × 4 actually measures 1.5 × 3.5 inches (3.7 × 8.8 centimeters) in width. Other commonly used dimensions are 2 × 3, 2 × 6, 2 × 8, 2 × 10, and 2 × 12, each of which are actually one-half to three-quarters of an inch thinner than the given dimensions. Dimensional lumber forms the major structural elements of floors, walls, joists, and rafters in home construction. Recently, the use of factory-made roof trusses built from dimensional wood materials provides for quick and easy construction of roof systems that are structurally strong and provide for free spans without the need for additional structural support from within the building. Construction workers or carpenters who erect the wooden frame of the building are called framers, and dimensional lumber is the material these people rely on for their livelihood.

Hardwoods

Woods that are used for building furniture, cabinetry, millwork, or other architectural features are typically hardwoods, although some conifer woods are also used for these items. Woods that are valued for furniture and cabinetry typically have aesthetically pleasing characteristics of uniform color, interesting patterns of earlywood and latewood in cut and surfaced lumber (this characteristic is termed grain or figure), and also possess desirable properties of hardness and durability. There are literally thousands of different species of hardwood (angiosperm) trees from around the world that have the potential for use in fine furniture and cabinetry; however, there are only relatively few species that are used commercially for this purpose. This is due to the requirement of having a reliable local source for adequate amounts of lumber (which differs in various parts of the world), the wood's machineability and finishing properties to provide a pleasing end-product, and consumers who favor certain wood species over others. In North America, the three major species used for furniture production are oak (*Quercus* spp., in particular, red oak), walnut (*Juglans* spp.), and cherry (*Prunus* spp.), which are more or less

A worker carving teak furniture at a factory in Chiang Mai, Thailand.

commonly available throughout the region. Many other species of hardwoods have similarly desirable properties, and furniture made from them is also valued; their use may reflect regional availability. Certain species of woods are also best suited to specific applications given their physical attributes. The strength and shock resistance of white ash (*Fraxinus americana*) makes it the wood of choice for the manufacture of baseball bats; rake, shovel, and other tool handles; and certain parts of chairs and other heavy-use furniture. Various species of maple (*Acer* spp.) are used for butcher blocks, bowling alley surfaces, bowling pins, the backs of violins, and various parts in the construction of pianos—all relying on maple's hard and durable characteristics.

Hardwoods are harvested in nearly every country capable of supporting a lumber industry. Thus, a considerable variety of wood species is available on the world lumber market. Those woods originating within the country of intended use are called domestic lumber, versus wood from those species obtained from foreign countries, which are called exotic woods. Hundreds of hardwood species are traded globally and have a diversity of color, grain, hardness, machineability, and finishing characteristics. One of the softest and lightest woods, balsa (*Ochroma lagopus*), a tropical species from South and Central America, is technically a hardwood, although it is much softer than most coniferous softwoods. Despite this fact, it is remarkably strong for its light weight, and modern uses for this wood include model building, insulation, and flotation devices. In contrast, one of the world's heaviest hardwoods is lignum vitae (*Guaiacum officinale*), another tropical tree species from the same general region as balsa. This wood has a specific gravity of 1.3 and will not float in water. The wood of lignum vitae is very heavy, and up to 30 percent of its weight is in the form of resins and oils. This wood resists decay very well and can withstand pressures of greater than 2,000 pounds per square inch. These characteristics make lignum vitae a very useful wood for various industrial, manufacturing, and marine applications. Some hardwoods are in plentiful supply, while others are uncommon or rare due to the relative scarcity of the species in natural forests. While many of these woods possess beautiful figure and color in their grain patterns and are highly sought by furniture builders, their continued harvest may pose problems in maintaining the tree species in its habitat, since many grow slowly and reproduce infrequently.

One way of using rare or uncommon hardwoods in furniture-making is through the process of veneering. Thin slices of highly desirable hardwoods are prepared and carefully dried. The dried wood slices (veneers) are glued to the surfaces of more common, structurally stable materials (such as plywood or fiberboard), and the veneer is protected with a suitable finish such as lacquer or varnish. The use of veneer saves valuable timber resources while enabling the enjoyment of beautiful grain and color characteristics of these hardwoods.

Lumber Production and Preparation

All production of wood products begins with the logging of timber by a number of methods (e.g., clear-cutting versus selective cutting). In intensively managed forest stands, softwood lumber (particularly dimension lumber or pulp lumber) can be produced quite efficiently. In contrast, the inherently slow growth of hardwood species restricts the methods of harvest primarily to selective methods from naturally occurring timber stands. Once logs have been felled and are ready for transport, they are moved from the timber stands by vehicle or by using waterways to float them to a milling operation. At the sawmill, the logs are sawn to optimize the quantity and quality of the lumber. The sawyer needs to know the characteristics of the wood being cut and how the lumber will respond to drying and further milling operations. When cut, live timber is very wet; the cell spaces in the xylem are filled with water (a moisture content of approximately 100 percent). This water (free water) must be removed; any remaining water within the cell wall complexes (bound water) must be removed so that the final moisture content of the wood is brought down to approximately 6 to 12 percent of the total weight of the dried wood.

Two main forms of drying wood are used. If an air-drying method is used, the rough-cut lumber is stacked with spacer boards (stickers) between the pieces of wood to promote air circulation around the boards. The lumber is then set out in open areas to allow the water to evaporate slowly from the cut surfaces of the wood, which eventually reduces the moisture content to an acceptable level. The other method uses a drying kiln—essentially a very large, forced-air oven in which temperature and air movement can be carefully controlled. The wet (or partially air-dried) stickered lumber is placed in the kiln, and the temperature and air circulation is increased to evaporate the water from within the wood; this process takes much less time than air-drying. When wood dries, it tends to shrink (particularly across the grain of the wood), so the kiln operator must be aware of the drying properties of each species of wood. If dried too quickly, the lumber can split, twist, or become damaged. When the wood has been sufficiently dried, it will remain relatively stable and is less likely to be attacked by wood rotting fungi when compared to wet woods. The dry, rough-cut lumber is then planed to final dimensions and is transported to distribution centers and lumber yards for use. Further processing of some woods is done with special rotary cutters to produce millwork, architectural trim pieces commonly used around doors and windows and along floors and ceilings. Other millwork items include railings, banisters, balusters, doors, and window frames—all essential components found in most traditionally built homes and other buildings.

Manufactured Wood Products

Some wood products are actually manufactured; that is, constructed from raw wood materials, but utilizing adhesives or other filler components to create new products useful to the construction industry. Perhaps the most important of these is plywood, a wood product made of several layers or plys of thinly cut wood. The grain patterns are normally oriented at right angles to one another prior to their lamination with various forms of adhesives. The result is a sheet stock product that is very dimensionally stable, maintains its flatness when installed properly, and can be used for a wide variety of applications: flooring, sheathing for the outer shell of framed buildings, and roofing. Development of plywood has revolutionized the home construction industry, which previously relied upon sawn and processed lumber planks for these purposes. Other manufactured wood products make use of chips, coarse wood particles, and, in some cases, wood fibers or sawdust, all of which were previously discarded as waste by-products of the lumber processing industry. Advances in wood technology have permitted the use of these materials with the addition of modern adhesives to produce products such as oriented strand board (OSB), particle board, and medium-density fiberboard (MDF). These are sheet-stock materials used in home construction, furniture manufacturing, and other industrial applications.

Other Wood Products

In addition to wood's uses for construction and furniture/cabinetry manufacture, other significant uses for wood products include the harvesting of wood for use by the pulp and paper industry, production of fibers for use in industry, conversion of raw wood materials into charcoal, extraction of turpentine and similar **compounds** for use as solvents and paint additives, and the use of cork in the beverage and manufacturing industries. Even the material previously stripped from the logs and discarded prior to transport to the mill is now used. Tree bark is a valued commodity for use in the landscaping/horticultural industry, and in some cases forms an organic component to artificial soil mixes. It is encouraging to note that today none of the parts of harvested trees are wasted—the technology of wood processing is sufficiently advanced to ensure that one of the world's most valuable and sustainable resources is used as efficiently as possible. Management of forests and natural habitats as sources of wood products is essential to provide for increasing needs of wood by humans. SEE ALSO CONIFERS; CORK; FIBER AND FIBER PRODUCTS; FORESTRY; PAPER; TREES; WOOD ANATOMY.

Robert S. Wallace

compound a substance formed from two or more elements

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Yeast

See Fungi.

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Glossary

abiotic nonliving

abrade to wear away through contact

abrasive tending to wear away through contact

abscission dropping off or separating

accession a plant that has been acquired and catalogued

achene a small, dry, thin-walled type of fruit

actinomycetes common name for a group of Gram-positive bacteria that are filamentous and superficially similar to fungi

addictive capable of causing addiction or chemical dependence

adhesion sticking to the surface of

adventitious arising from secondary buds, or arising in an unusual position

aeration the introduction of air

albuminous gelatinous, or composed of the protein albumin

alkali chemically basic; the opposite of acidic

alkalinization increase in basicity or reduction in acidity

alkaloid bitter secondary plant compound, often used for defense

allele one form of a gene

allelopathy harmful action by one plant against another

allopolyploidy a polyploid organism formed by hybridization between two different species or varieties (*allo* = other)

alluvial plain broad area formed by the deposit of river sediment at its outlet

amended soils soils to which fertilizers or other growth aids have been added

amendment additive

anaerobic without oxygen

analgesic pain-relieving

analog a structure or thing, especially a chemical, similar to something else

angiosperm a flowering plant

anomalous unusual or out of place

anoxic without oxygen

antenna system a collection of protein complexes that harvests light energy and converts it to excitation energy that can migrate to a reaction center; the light is absorbed by pigment molecules (e.g., chlorophyll, carotenoids, phycobilin) that are attached to the protein

anthropogenic human-made; related to or produced by the influence of humans on nature

antibodies proteins produced to fight infection

antioxidant a substance that prevents damage from oxygen or other reactive substances

apical meristem region of dividing cells at the tips of growing plants

apical at the tip

apomixis asexual reproduction that may mimic sexual reproduction

appendages parts that are attached to a central stalk or axis

arable able to be cultivated for crops

Arcto-Tertiary geoflora the fossil flora discovered in Arctic areas dating back to the Tertiary period; this group contains magnolias (*Magnolia*), tulip trees (*Liriodendron*), maples (*Acer*), beech (*Fagus*), black gum (*Nyssa*), sweet gum (*Liquidambar*), dawn redwood (*Metasequoia*), cypress (*Taxodium*), and many other species

artifacts pots, tools, or other cultural objects

assayer one who performs chemical tests to determine the composition of a substance

ATP adenosine triphosphate, a small, water-soluble molecule that acts as an energy currency in cells

attractant something that attracts

autotroph "self-feeder"; any organism that uses sunlight or chemical energy

auxin a plant hormone

avian related to birds

axil the angle or crotch where a leaf stalk meets the stem

axillary bud the bud that forms in the angle between the stem and leaf

basipetal toward the base

belladonna the source of atropine; means "beautiful woman," and is so named because dilated pupils were thought to enhance a woman's beauty

binomial two-part

biodirected assays tests that examine some biological property

biodiversity degree of variety of life

biogeography the study of the reasons for the geographic distribution of organisms

biomass the total dry weight of an organism or group of organisms

biosphere the region of the Earth in which life exists

biosynthesis creation through biological pathways

biota the sum total of living organisms in a region of a given size

biotic involving or related to life

bryologist someone who studies bryophytes, a division of nonflowering plants

campanulate bell-shaped

capitulum the head of a compound flower, such as a dandelion

cardiotonic changing the contraction properties of the heart

carotenoid a yellow-colored molecule made by plants

carpels the innermost whorl of flower parts, including the egg-bearing ovules, plus the style and stigma attached to the ovules

catastrophism the geologic doctrine that sudden, violent changes mark the geologic history of Earth

cation positively charged particle

catkin a flowering structure used for wind pollination

centrifugation spinning at high speed in a centrifuge to separate components

chitin a cellulose-like molecule found in the cell wall of many fungi and arthropods

chloroplast the photosynthetic organelle of plants and algae

circadian "about a day"; related to a day

circumscription the definition of the boundaries surrounding an object or an idea

cisterna a fluid-containing sac or space

clade a group of organisms composed of an ancestor and all of its descendants

cladode a modified stem having the appearance and function of a leaf

coalescing roots roots that grow together

coleoptile the growing tip of a monocot seedling

collenchyma one of three cell types in ground tissue

colonize to inhabit a new area

colony a group of organisms inhabiting a particular area, especially organisms descended from a common ancestor

commensalism a symbiotic association in which one organism benefits while the other is unaffected

commodities goods that are traded, especially agricultural goods

community a group of organisms of different species living in a region

compaction compacting of soil, leading to the loss of air spaces

complex hybrid hybridized plant having more than two parent plants

compound a substance formed from two or more elements

concentration gradient a difference in concentration between two areas

continental drift the movement of continental land masses due to plate tectonics

contractile capable of contracting

convective uplift the movement of air upwards due to heating from the sun

coppice growth the growth of many stems from a single trunk or root, following the removal of the main stem

cortical relating to the cortex of a plant

covalent held together by electron-sharing bonds

crassulacean acid metabolism water-conserving strategy used by several types of plants

crop rotation alternating crops from year to year in a particular field

cultivation growth of plants, or turning the soil for growth of crop plants

crystallography the use of x-rays on crystals to determine molecular structure

cuticle the waxy outer coating of a leaf or other structure, which provides protection against predators, infection, and water loss

cyanide heap leach gold mining a technique used to extract gold by treating ore with cyanide

cyanobacteria photosynthetic prokaryotic bacteria formerly known as blue-green algae

cyanogenic giving rise to cyanide

cytologist a scientist who studies cells

cytology the microscopic study of cells and cell structure

cytosol the fluid portion of a cell

cytostatic inhibiting cell division

deductive reasoning from facts to conclusion

dendrochronologist a scientist who uses tree rings to determine climate or other features of the past

dermatophytes fungi that cause skin diseases

desertification degradation of dry lands, reducing productivity

desiccation drying out

detritus material from decaying organisms

diatoms hard-shelled, single-celled marine organisms; a type of algae

dictyosome any one of the membranous or vesicular structures making up the Golgi apparatus

dioicous having male and female sexual parts on different plants

diploid having two sets of chromosomes, versus having one set (haploid)

dissipate to reduce by spreading out or scattering

distal further away from

diurnal daily, or by day

domestication the taming of an organism to live with and be of use to humans

dormant inactive, not growing

drupe a fruit with a leathery or stone-like seed

dynamical system theory the mathematical theory of change within a system

ecophysiological related to how an organism's physiology affects its function in an ecosystem

ecosystem an ecological community and its environment

elater an elongated, thickened filament

empirical formula the simplest whole number ratio of atoms in a compound

emulsifier a chemical used to suspend oils in water

encroachment moving in on

endemic belonging or native to a particular area or country

endophyte a fungus that lives within a plant

endoplasmic reticulum the membrane network inside a cell

endosperm the nutritive tissue in a seed, formed by the fertilization of a diploid egg tissue by a sperm from pollen

endosporic the formation of a gametophyte inside the spore wall

endosymbiosis a symbiosis in which one organism lives inside the other

Enlightenment eighteenth-century philosophical movement stressing rational critique of previously accepted doctrines in all areas of thought

entomologist a scientist who studies insects

enzyme a protein that controls a reaction in a cell

ephemeral short-lived

epicuticle the waxy outer covering of a plant, produced by the epidermis

epidermis outer layer of cells

epiphytes plants that grow on other plants

escarpment a steep slope or cliff resulting from erosion

ethnobotanist a scientist who interacts with native peoples to learn more about the plants of a region

ethnobotany the study of traditional uses of plants within a culture

euglossine bees a group of bees that pollinate orchids and other rainforest plants

eukaryotic a cell with a nucleus (*eu* means "true" and *karyo* means "nucleus"); includes protists, plants, animals, and fungi

extrafloral outside the flower

exudation the release of a liquid substance; oozing

facultative capable of but not obligated to

fertigation application of small amounts of fertilizer while irrigating

filament a threadlike extension

filamentous thin and long

flagella threadlike extension of the cell membrane, used for movement

flavonoids aromatic compounds occurring in both seeds and young roots and involved in host-pathogen and host-symbiont interactions

florigen a substance that promotes flowering

floristic related to plants

follicle sac or pouch

forbs broad-leaved, herbaceous plants

free radicals toxic molecular fragments

frugivous feeding on fruits

gametangia structure where gametes are formed

gametophyte the haploid organism in the life cycle

gel electrophoresis a technique for separating molecules based on size and electrical charge

genera plural of genus; a taxonomic level above species

genome the genetic material of an organism

genotype the genetic makeup of an organism

germplasm hereditary material, especially stored seed or other embryonic forms

globose rounded and swollen; globe-shaped

gradient difference in concentration between two places

green manure crop planted to be plowed under to nourish the soil, especially with nitrogen

gymnosperm a major group of plants that includes the conifers

gynoecium the female reproductive organs as a whole

gypsipherous containing the mineral gypsum

hallucinogenic capable of inducing hallucinations

haploid having one set of chromosomes, versus having two (diploid)

haustorial related to a haustorium, or food-absorbing organ

hemiterpene a half terpene

herbivore an organism that feeds on plant parts

heterocyclic a chemical ring structure composed of more than one type of atom, for instance carbon and nitrogen

heterosporous bearing spores of two types, large megaspores and small microspores

heterostylous having styles (female flower parts) of different lengths, to aid cross-pollination

heterotroph an organism that derives its energy from consuming other organisms or their body parts

holistic including all the parts or factors that relate to an object or idea

homeotic relating to or being a gene that produces a shift in structural development

homology a similarity in structure between anatomical parts due to descent from a common ancestor

humus the organic material in soil formed from decaying organisms

hybrid a mix of two varieties or species

hybridization formation of a new individual from parents of different species or varieties

hydrological cycle the movement of water through the biosphere

hydrophobic water repellent

hydroponic growing without soil, in a watery medium

hydroxyl the chemical group -OH

hyphae the threadlike body mass of a fungus

illicit illegal

impede to slow down or inhibit

inert incapable of reaction

inflorescence a group of flowers or arrangement of flowers in a flower head

infrastructure roads, phone lines, and other utilities that allow commerce

insectivorous insect-eating

intercalary inserted; between

interspecific hybridization hybridization between two species

intertidal between the lines of high and low tide

intracellular bacteria bacteria that live inside other cells

intraspecific taxa levels of classification below the species level

intuiting using intuition

ionic present as a charged particle

ions charged particles

irreversible unable to be reversed

juxtaposition contrast brought on by close positioning

lacerate cut

Lamarckian inheritance the hypothesis that acquired characteristics can be inherited

lamellae thin layers or plate-like structure

land-grant university a state university given land by the federal government on the condition that it offer courses in agriculture

landrace a variety of a cultivated plant, occurring in a particular region

lateral to the side of

legume beans and other members of the Fabaceae family

lignified composed of lignin, a tough and resistant plant compound

lineage ancestry; the line of evolutionary descent of an organism

loci (singular: locus) sites or locations

lodging falling over while still growing

lytic breaking apart by the action of enzymes

macromolecule a large molecule such as a protein, fat, nucleic acid, or carbohydrate

macroscopic large, visible

medulla middle part

megaphylls large leaves having many veins or a highly branched vein system

meiosis the division of chromosomes in which the resulting cells have half the original number of chromosomes

meristem the growing tip of a plant

mesic of medium wetness

microfibrils microscopic fibers in a cell

micron one millionth of a meter; also called micrometer

microphylls small leaves having a single unbranched vein

mitigation reduction of amount or effect

mitochondria cell organelles that produce adenosine triphosphate (ATP) to power cell reactions

mitosis the part of the cell cycle in which chromosomes are separated to give each daughter cell an identical chromosome set

molecular systematics the analysis of DNA and other molecules to determine evolutionary relationships

monoculture a large stand of a single crop species

monomer a single unit of a multi-unit structure

monophyletic a group that includes an ancestral species and all its descendants

montane growing in a mountainous region

morphology shape and form

motile capable of movement

mucilaginous sticky or gummy

murein a peptidoglycan, a molecule made up of sugar derivatives and amino acids

mutualism a symbiosis between two organisms in which both benefit

mycelium the vegetative body of a fungus, made up of threadlike hyphae

$NADP^+$ oxidized form of nicotinamide adenine dinucleotide phosphate

NADPH reduced form of nicotinamide adenine dinucleotide phosphate, a small, water-soluble molecule that acts as a hydrogen carrier in biochemical reactions

nanometer one billionth of a meter

nectaries organs in flowers that secrete nectar

negative feedback a process by which an increase in some variable causes a response that leads to a decrease in that variable

neuromuscular junction the place on the muscle surface where the muscle receives stimulus from the nervous system

neurotransmitter a chemical that passes messages between nerve cells

node branching site on a stem

nomenclature a naming system

nonmotile not moving

nonpolar not directed along the root-shoot axis, or not marked by separation of charge (unlike water and other polar substances)

nonsecretory not involved in secretion, or the release of materials

Northern Blot a technique for separating RNA molecules by electrophoresis and then identifying a target fragment with a DNA probe

nucleolar related to the nucleolus, a distinct region in the nucleus

nurseryman a worker in a plant nursery

obligate required, without another option

obligate parasite a parasite without a free-living stage in the life cycle

odorant a molecule with an odor

organelle a membrane-bound structure within a cell

osmosis the movement of water across a membrane to a region of high solute concentration

oviposition egg-laying

oxidation reaction with oxygen, or loss of electrons in a chemical reaction

paleobotany the study of ancient plants and plant communities

pangenesis the belief that acquired traits can be inherited by bodily influences on the reproductive cells

panicle a type of inflorescence (flower cluster) that is loosely packed and irregularly branched

paraphyletic group a taxonomic group that excludes one or more descendants of a common ancestor

parenchyma one of three types of cells found in ground tissue

pastoralists farming people who keep animal flocks

pathogen disease-causing organism

pedicel a plant stalk that supports a fruiting or spore-bearing organ

pentamerous composed of five parts

percolate to move through, as a fluid through a solid

peribacteroid a membrane surrounding individual or groups of rhizobia bacteria within the root cells of their host; in such situations the bacteria

have frequently undergone some change in surface chemistry and are referred to as bacteroids

pericycle cell layer between the conducting tissue and the endodermis

permeability the property of being permeable, or open to the passage of other substances

petiole the stalk of a leaf, by which it attaches to the stem

pH a measure of acidity or alkalinity; the pH scale ranges from 0 to 14, with 7 being neutral. Low pH numbers indicate high acidity while high numbers indicate alkalinity

pharmacognosy the study of drugs derived from natural products

pharmacopeia a group of medicines

phenology seasonal or other time-related aspects of an organism's life

pheromone a chemical released by one organism to influence the behavior of another

photooxidize to react with oxygen under the influence of sunlight

photoperiod the period in which an organism is exposed to light or is sensitive to light exposure, causing flowering or other light-sensitive changes

photoprotectant molecules that protect against damage by sunlight

phylogenetic related to phylogeny, the evolutionary development of a species

physiology the biochemical processes carried out by an organism

phytogeographer a scientist who studies the distribution of plants

pigments colored molecules

pistil the female reproductive organ of a flower

plasmodesmata cell-cell junctions that allow passage of small molecules between cells

polyculture mixed species

polyhedral in the form of a polyhedron, a solid whose sides are polygons

polymer a large molecule made from many similar parts

polynomial "many-named"; a name composed of several individual parts

polyploidy having multiple sets of chromosomes

polysaccharide a linked chain of many sugar molecules

population a group of organisms of a single species that exist in the same region and interbreed

porosity openness

positive feedback a process by which an increase in some variable causes a response that leads to a further increase in that variable

precipitation rainfall; or the process of a substance separating from a solution

pre-Columbian before Columbus

precursor a substance from which another is made

predation the act of preying upon; consuming for food

primordial primitive or early

progenitor parent or ancestor

prokaryotes single-celled organisms without nuclei, including Eubacteria and Archaea

propagate to create more of through sexual or asexual reproduction

protist a usually single-celled organism with a cell nucleus, of the kingdom Protista

protoplasmic related to the protoplasm, cell material within the cell wall

protoplast the portion of a cell within the cell wall

psychoactive causing an effect on the brain

pubescence covered with short hairs

pyruvic acid a three-carbon compound that forms an important intermediate in many cellular processes

quadruple hybrid hybridized plant with four parents

quantitative numerical, especially as derived from measurement

quid a wad for chewing

quinone chemical compound found in plants, often used in making dyes

radii distance across, especially across a circle (singular = radius)

radioisotopes radioactive forms of an element

rambling habit growing without obvious intended direction

reaction center a protein complex that uses light energy to create a stable charge separation by transferring a single electron energetically uphill from a donor molecule to an acceptor molecule, both of which are located in the reaction center

redox oxidation and reduction

regurgitant material brought up from the stomach

Renaissance a period of artistic and intellectual expansion in Europe from the fourteenth to the sixteenth century

salinization increase in salt content

samara a winged seed

saprophytes plants that feed on decaying parts of other plants

saturated containing as much dissolved substance as possible

sclerenchyma one of three cell types in ground tissue

sedimentation deposit of mud, sand, shell, or other material

semidwarf a variety that is intermediate in size between dwarf and full-size varieties

senescent aging or dying

sepals the outermost whorl of flower parts; usually green and leaf-like, they protect the inner parts of the flower

sequester to remove from circulation; lock up

serology the study of serum, the liquid, noncellular portion of blood

seta a stiff hair or bristle

silage livestock food produced by fermentation in a silo

siliceous composed of silica, a mineral

silicified composed of silicate minerals

soil horizon distinct layers of soil

solute a substance dissolved in a solution

Southern blot a technique for separating DNA fragments by electrophoresis and then identifying a target fragment with a DNA probe

spasticity abnormal muscle activity caused by damage to the nerve pathways controlling movement

speciation the creation of new species

specimen an object or organism under consideration

speciose marked by many species

sporophyte the diploid, spore-producing individual in the plant life cycle

sporulate to produce or release spores

sterile not capable or involved in reproduction, or unable to support life

sterols chemicals related to steroid hormones

stolons underground stems that may sprout and form new individuals

stomata openings between guard cells on the underside of leaves that allow gas exchange

stratification layering, or separation in space

stratigraphic geology the study of rock layers

stratigraphy the analysis of strata (layered rock)

strobili cone-like reproductive structures

subalpine a region less cold or elevated than alpine (mountaintop)

substrate the physical structure to which an organism attaches, or a molecule acted on by enzymes

succession the pattern of changes in plant species that occurs after a soil disturbance

succulent fleshy, moist

suckers naturally occuring adventitious shoots

suffrutescent a shrub-like plant with a woody base

sulfate a negatively charged particle combining sulfur and oxygen

surfaced smoothed for examination

susceptibility vulnerability

suture line of attachment

swidden agriculture the practice of farming an area until the soil has been depleted and then moving on

symbiont one member of a symbiotic association

symbiosis a relationship between organisms of two different species in which at least one benefits

systematists scientists who study systematics, the classification of species to reflect evolutionary relationships

systemic spread throughout the plant

tannins compounds produced by plants that usually serve protective functions, often colored and used for "tanning" and dyeing

taxa a type of organism, or a level of classification of organisms

tensile forces forces causing tension, or pulling apart; the opposite of compression

tepal an undifferentiated sepal or petal

Tertiary period geologic period from sixty-five to five million years ago

tetraploid having four sets of chromosomes; a form of polyploidy

thallus simple, flattened, nonleafy plant body

tilth soil structure characterized by open air spaces and high water storage capacity due to high levels of organic matter

tonoplast the membrane of the vacuole

topographic related to the shape or contours of the land

totipotent capable of forming entire plants from individual cells

toxin a poisonous substance

tracheid a type of xylem cell that conducts water from root to shoot

transcription factors proteins that bind to a specific DNA sequence called the promoter to regulate the expression of a nearby gene

translocate to move materials from one region to another

translucent allowing the passage of light

transmutation to change from one form to another

transpiration movement of water from soil to atmosphere through a plant

transverse across, or side to side

tribe a group of closely related genera

trophic related to feeding

turgor pressure the outward pressure exerted on the cell wall by the fluid within

twining twisting around while climbing

ultrastructural the level of structure visible with the electron microscope; very small details of structure

uniformitarian the geologic doctrine that formative processes on earth have proceeded at the same rate through time since earth's beginning

uplift raising up of rock layers, a geologic process caused by plate tectonics

urbanization increase in size or number of cities

vacuole the large fluid-filled sac that occupies most of the space in a plant cell. Used for storage and maintaining internal pressure

vascular plants plants with specialized transport cells; plants other than bryophytes

vascular related to the transport of nutrients, or related to blood vessels

vector a carrier, usually one that is not affected by the thing carried

vernal related to the spring season

vesicle a membrane-bound cell structure with specialized contents

viable able to live or to function

volatile easily released as a gas

volatilization the release of a gaseous substance

water table the level of water in the soil

whorl a ring

wort an old English term for plant; also an intermediate liquid in beer making

xenobiotics biomolecules from outside the plant, especially molecules that are potentially harmful

xeromorphic a form adapted for dry conditions

xerophytes plants adapted for growth in dry areas

zonation division into zones having different properties

zoospore a swimming spore

zygote the egg immediately after it has been fertilized; the one-cell stage of a new individual

Topic Outline

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Alkaloids
Allelopathy
Cacti
Cells, Specialized Types
Clines and Ecotypes
Defenses, Chemical
Defenses, Physical
Halophytes
Lichens
Mycorrhizae
Nitrogen Fixation
Poisonous Plants
Seed Dispersal
Shape and Form of Plants
Symbiosis
Translocation
Trichomes

AGRICULTURE

Agriculture, History of
Agriculture, Modern
Agriculture, Organic
Agricultural Ecosystems
Agronomist
Alliaceae
Asteraceae
Biofuels
Borlaug, Norman
Breeder
Breeding
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Cacao
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Coffee
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Economic Importance of Plants
Ethnobotany
Fertilizer
Fiber and Fiber Products
Food Scientist
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Fruits, Seedless
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Genetic Engineering
Grains
Grasslands
Green Revolution
Halophytes
Herbs and Spices
Herbicides
Horticulture
Horticulturist
Hydroponics
Native Food Crops
Nitrogen Fixation
Oils, Plant-Derived
Pathogens
Pathologist
Polyploidy
Potato
Potato Blight
Quantitative Trait Loci
Rice
Seed Preservation
Soil, Chemistry of
Soil, Physical Characteristics
Solanaceae
Soybeans
Sugar
Tea
Tissue Culture

Tobacco
Transgenic Plants
Vavilov, N. I.
Vegetables
Weeds
Wheat
Wine and Beer Industry

ANATOMY

Anatomy of Plants
Bark
Botanical and Scientific Illustrator
Cell Walls
Cells
Cells, Specialized Types
Cork
Differentiation and Development
Fiber and Fiber Products
Flowers
Fruits
Inflorescence
Leaves
Meristems
Mycorrhizae
Phyllotaxis
Plants
Roots
Seeds
Shape and Form of Plants
Stems
Tissues
Tree Architecture
Trichomes
Vascular Tissues
Vegetables
Wood Anatomy

BIOCHEMISTRY/PHYSIOLOGY

Alcoholic Beverage Industry
Alkaloids
Anthocyanins
Biofuels
Biogeochemical Cycles
Bioremediation
Carbohydrates
Carbon Cycle
Cells
Cellulose
Chlorophyll
Chloroplasts
Cytokinins
Defenses, Chemical
Ecology, Energy Flow
Fertilizer
Flavonoids
Flavor and Fragrance Chemist
Halophytes
Herbicides
Hormones
Lipids
Medicinal Plants
Nitrogen Fixation
Nutrients
Oils, Plant-Derived
Pharmaceutical Scientist
Photoperiodism
Photosynthesis, Carbon Fixation
Photosynthesis, Light Reactions
Physiologist
Pigments
Poisonous Plants
Psychoactive Plants
Soil, Chemistry of
Terpenes
Translocation
Vacuoles
Water Movement

BIODIVERSITY

Agricultural Ecosystems
Aquatic Ecosystems
Biodiversity
Biogeography
Biome
Botanical Gardens and Arboreta
Chapparal
Clines and Ecotypes
Coastal Ecosystems
Coniferous Forests
Curator of a Botanical Garden
Curator of an Herbarium
Deciduous Forests
Deforestation
Desertification
Deserts
Ecology
Ethnobotany
Global Warning
Herbaria
Human Impacts
Invasive Species

Plant Prospecting
Rain Forest Canopy
Rain Forests
Savanna
Taxonomist
Tundra
Wetlands

BIOMES

Aquatic Ecosystems
Atmosphere and Plants
Biodiversity
Biogeography
Biome
Cacti
Chapparal
Coastal Ecosystems
Coniferous Forests
Deciduous Forests
Deforestation
Desertification
Deserts
Ecology
Ecosystem
Global Warning
Grasslands
Human Impacts
Invasive Species
Peat Bogs
Plant Prospecting
Rain Forest Canopy
Rain Forests
Savanna
Tundra
Wetlands

CAREERS

Agriculture, Modern
Agriculture, Organic
Agronomist
Alcoholic Beverage Industry
Arborist
Botanical and Scientific Illustrator
Breeder
Breeding
College Professor
Curator of a Botanical Garden
Curator of an Herbarium
Flavor and Fragrance Chemist
Food Scientist
Forester
Forestry
Genetic Engineer
Genetic Engineering
Horticulture
Horticulturist
Landscape Architect
Pathologist
Pharmaceutical Scientist
Physiologist
Plant Prospecting
Taxonomist
Turf Management

CELL BIOLOGY

Algae
Biogeochemical Cycles
Cell Cycle
Cell Walls
Cells
Cells, Specialized Types
Cellulose
Chloroplasts
Cork
Differentiation and Development
Embryogenesis
Fiber and Fiber Products
Germination
Germination and Growth
Leaves
Meristems
Molecular Plant Genetics
Mycorrhizae
Nitrogen Fixation
Physiologist
Plastids
Reproduction, Fertilization
Roots
Seeds
Stems
Tissues
Translocation
Trichomes
Tropisms and Nastic Movements
Vacuoles
Vascular Tissues
Water Movement
Wood Anatomy

DESERTS

Biome
Cacti

Desertification
Deserts
Ecosystem
Halophytes
Native Food Crops
Photosynthesis, Carbon Fixation and
Tundra

DISEASES OF PLANTS

Acid Rain
Chestnut Blight
Deforestation
Dutch Elm Disease
Fungi
Interactions, Plant-Fungal
Interactions, Plant-Insect
Nutrients
Pathogens
Pathologist
Potato Blight

DRUGS AND POISONS

Alcoholic Beverage Industry
Alcoholic Beverages
Alkaloids
Cacao
Cannabis
Coca
Coffee
Defenses, Chemical
Dioscorea
Economic Importance of Plants
Ethnobotany
Flavonoids
Medicinal Plants
Pharmaceutical Scientist
Plant Prospecting
Poison Ivy
Poisonous Plants
Psychoactive Plants
Solanaceae
Tea
Tobacco

ECOLOGY

Acid Rain
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Aquatic Ecosystems
Atmosphere and Plants
Biodiversity
Biogeochemical Cycles
Biogeography
Biome
Carbon Cycle
Chapparal
Clines and Ecotypes
Coastal Ecosystems
Coniferous Forests
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Decomposers
Defenses, Chemical
Defenses, Physical
Deforestation
Desertification
Deserts
Ecology
Ecology, Energy Flow
Ecology, Fire
Ecosystem
Endangered Species
Global Warning
Grasslands
Human Impacts
Interactions, Plant-Fungal
Interactions, Plant-Insect
Interactions, Plant-Plant
Interactions, Plant-Vertebrate
Invasive Species
Mycorrhizae
Nutrients
Pathogens
Peat Bogs
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Rain Forest Canopy
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ECONOMIC IMPORTANCE OF PLANTS

Acid Rain
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Arborist
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Agriculture, Modern
Agriculture, Organic

Alcoholic Beverage Industry
Alcoholic Beverages
Bamboo
Biofuels
Bioremediation
Breeder
Cacao
Cannabis
Chestnut Blight
Coffee
Coniferous Forests
Cork
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Fiber and Fiber Products
Flavor and Fragrance Chemist
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Forensic Botany
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Human Impacts
Hydroponics
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Oils, Plant-Derived
Ornamental Plants
Paper
Peat Bogs
Pharmaceutical Scientist
Plant Prospecting
Potato Blight
Rice
Soybeans
Sugar
Tea
Turf Management
Wheat
Wood Products
Vegetables

EVOLUTION

Algae
Angiosperms
Archaea
Biodiversity
Biogeography
Breeding Systems
Bryophytes
Clines and Ecotypes
Curator of an Herbarium
Darwin, Charles
Defenses, Chemical
Defenses, Physical
Endangered Species
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Eubacteria
Ferns
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Poisonous Plants
Pollination Biology
Polyploidy
Reproduction, Alternation of Generations
Seed Dispersal
Speciation
Symbiosis
Systematics, Molecular
Systematics, Plant
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FOODS

Alcoholic Beverage Industry
Alliaceae
Bamboo
Cacao
Cacti
Carbohydrates
Coffee
Corn

Fruits
Fruits, Seedless
Grains
Herbs and Spices
Leaves
Native Food Crops
Oils, Plant-Derived
Rice
Roots
Seeds
Solanaceae
Soybeans
Stems
Sugar
Tea
Wheat

GARDENING

Alliaceae
Compost
Flowers
Fruits
Herbicides
Horticulture
Invasive Species
Landscape Architect
Ornamental Plants
Vegetables

GENETICS

Breeder
Breeding
Breeding Systems
Cell Cycle
Chromosomes
Fruits, Seedless
Genetic Engineer
Genetic Engineering
Genetic Mechanisms and Development
Green Revolution
Hormonal Control and Development
Molecular Plant Genetics
Polyploidy
Quantitative Trait Loci
Reproduction, Alternation of Generations
Reproduction, Asexual
Reproduction, Fertilization
Reproduction, Sexual
Transgenic Plants

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Borlaug, Norman
Britton, Nathaniel
Brongniart, Adolphe-Theodore
Burbank, Luther
Calvin, Melvin
Carver, George W.
Clements, Frederic
Cordus, Valerius
Creighton, Harriet
Darwin, Charles
de Candolle, Augustin
de Saussure, Nicholas
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Evolution of Plants, History of
Gray, Asa
Green Revolution
Hales, Stephen
Herbals and Herbalists
Hooker, Joseph Dalton
Humboldt, Alexander von
Ingenhousz, Jan
Linneaus, Carolus
McClintock, Barbara
Mendel, Gregor
Odum, Eugene
Physiology, History of
Sachs, Julius von
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Torrey, John
Van Helmont, Jean Baptiste
van Niel, C. B.
Vavilov, N. I.
Warming, Johannes

HORMONES

Differentiation and Development
Genetic Mechanisms and Development
Herbicides
Hormonal Control and Development
Hormones
Meristems
Photoperiodism
Physiologist
Rhythms in Plant Life
Senescence
Shape and Form of Plants
Tropisms and Nastic Movements

HORTICULTURE

Alliaceae
Asteraceae
Bonsai
Botanical Gardens and Arboreta
Breeder
Breeding
Cacti
Curator of a Botanical Garden
Horticulture
Horticulturist
Hybrids and Hybridization
Hydroponics
Landscape Architect
Ornamental Plants
Polyploidy
Propagation
Turf Management

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