Second Edition

INSECT ECOLOGY

An Ecosystem Approach

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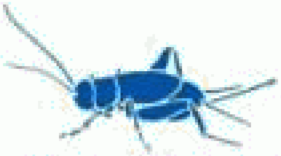

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PREFACE

This second edition provides an updated and expanded synthesis of feedbacks and interactions between insects and their environment. A number of recent studies have advanced understanding of feedbacks or provided useful examples of principles. Molecular methods have provided new tools for addressing dispersal and interactions among organisms and have clarified mechanisms of feedback between insect effects on, and responses to, environmental changes. Recent studies of factors controlling energy and nutrient fluxes have advanced understanding and prediction of interactions among organisms and abiotic nutrient pools.

The traditional focus of insect ecology has provided valuable examples of adaptation to environmental conditions and evolution of interactions with other organisms. By contrast, research at the ecosystem level in the last 3 decades has addressed the integral role of herbivores and detritivores in shaping ecosystem conditions and contributing to energy and matter fluxes that influence global processes. This text is intended to provide a modern perspective of insect ecology that integrates these two traditions to approach the study of insect adaptations from an ecosystem context. This integration substantially broadens the scope of insect ecology and contributes to prediction and resolution of the effects of current environmental changes as these affect and are affected by insects.

This text demonstrates how evolutionary and ecosystem approaches complement each other, and is intended to stimulate further integration of these approaches in experiments that address insect roles in ecosystems. Both approaches are necessary to understand and predict the consequences of environmental changes, including anthropogenic changes, for insects and their contributions to ecosystem structure and processes (such as primary productivity, biogeochemical cycling, carbon flux, and community dynamics). Effective management of ecosystem resources depends on evaluation of the complex, often complementary, effects of insects on ecosystem conditions as well as insect responses to changing conditions.

Two emerging needs require the integration of traditional and emerging perspectives of insect roles in ecosystems. First, we are becoming increasingly aware that global environmental changes must be addressed from a global (rather than local) perspective, with emphasis on integrating ecological processes at various levels of resolution and across regional landscapes. Insect population structure, interactions with other species, and effects on ecosystem processes are integral to explaining and mitigating global changes. Second, the changing goals of natural resource management require a shift in emphasis from the traditional focus on insect–plant interactions and crop "protection" to an integration of ecosystem components and processes that affect sustainability of ecosystem conditions and products. Integrated pest management (IPM) is founded on such ecological principles.

The hierarchical model, familiar to ecosystem ecologists and used in this text, focuses on linkages and feedbacks among individual, population, community, and ecosystem properties. This model contributes to integration of evolutionary and ecosystem approaches by illustrating how properties at higher levels of resolution (e.g., the community or ecosystem) contribute to the environment perceived at lower levels (e.g., populations and individuals) and how responses at lower levels contribute to properties at higher levels of this hierarchy. Some overlap among sections and chapters is necessary to emphasize linkages among levels. Where possible, overlap is minimized through cross-referencing.

A number of colleagues have contributed enormously to my perspectives on insect and ecosystem ecology. I am especially grateful to J. T. Callahan, J.-T. Chao, S. L. Collins, R. N. Coulson, D. A. Crossley, Jr., R. Dame, D. A. Distler, L. R. Fox, J. F. Franklin, F. B. Golley, J. R. Gosz, M. D. Hunter, F. Kozár, M. D. Lowman, G. L. Lovett, H.-K. Luh, J. C. Moore, E. P. Odum, H. T. Odum, D. W. Roubik, T. R. Seastedt, D. J. Shure, P. Turchin, R. B. Waide, W. G. Whitford, R. G. Wiegert, M. R. Willig, and W.-J. Wu for sharing ideas, data, and encouragement. I also have benefited from collaboration with colleagues at Louisiana State University and Oregon State University and associated with U.S. Long Term Ecological Research (LTER) sites, International LTER projects in Hungary and Taiwan, the Smithsonian Tropical Research Institute, Wind River Canopy Crane Research Facility, Teakettle Experimental Forest, USDA Forest Service Demonstration of Ecosystem Management Options (DEMO) Project, USDA Western Regional Project on Bark Beetle-Pathogen Interactions, and the National Science Foundation. L. R. Fox, T. R. Seastedt, and M. R. Willig reviewed drafts of the previous edition. Several anonymous reviewers provided useful comments addressed in this edition. I also am indebted to C. Schowalter for encouragement and feedback. K. Sonnack, B. Siebert and H. Furrow at Elsevier provided valuable editorial assistance. I am, of course, solely responsible for the selection and organization of material in this book.

1

Overview

INSECTS ARE THE DOMINANT GROUP OF ORGANISMS ON EARTH, IN terms of both taxonomic diversity (>50% of all described species) and ecological function (E. Wilson 1992) (Fig. 1.1). Insects represent the vast majority of species in terrestrial and freshwater ecosystems and are important components of nearshore marine ecosystems as well. This diversity of insect species represents an equivalent variety of adaptations to variable environmental conditions. Insects affect other species (including humans) and ecosystem parameters in a variety of ways. The capacity for rapid response to environmental change makes insects useful indicators of change, major engineers and potential regulators of ecosystem conditions, and frequent competitors with human demands for ecosystem resources or vectors of human and animal diseases.

Insects also play critical roles in ecosystem function. They represent important food resources or disease vectors for many other organisms, including humans, and they have the capacity to alter rates and directions of energy and matter fluxes (e.g., as herbivores, pollinators, detritivores, and predators) in ways that potentially affect global processes. In some ecosystems, insects and other arthropods represent the dominant pathways of energy and matter flow, and their biomass may exceed that of the more conspicuous vertebrates (e.g., Whitford 1986). Some species are capable of removing virtually all vegetation from a site. They affect, and are affected by, environmental issues as diverse as ecosystem health, air and water quality, genetically modified crops, disease epidemiology, frequency and severity of fire and other disturbances, control of invasive exotic species, land use, and climate change. Environmental changes, especially those resulting from anthropogenic activities, affect abundances of many species in ways that alter ecosystem and, perhaps, global processes.

A primary challenge for insect ecologists is to place insect ecology in an ecosystem context that represents insect effects on ecosystem properties, as well

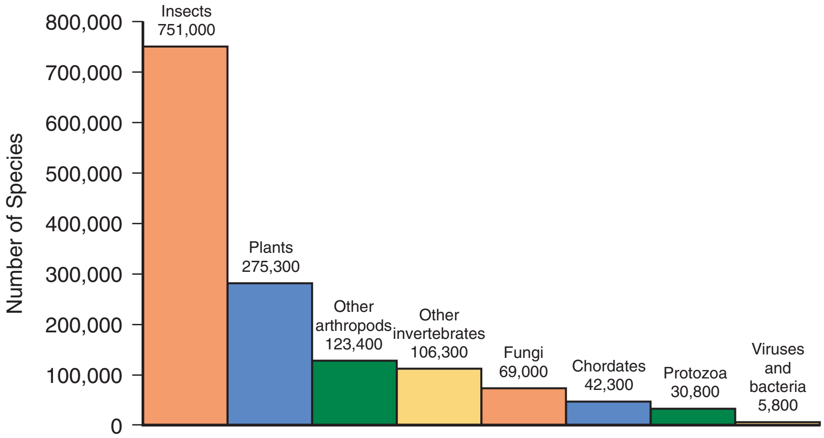


FIG. 1.1 Distribution of described species within major taxonomic groups. Species numbers for insects, bacteria, and fungi likely will increase greatly as these groups become better known. Data from E. O. Wilson (1992).

as the diversity of their adaptations and responses to environmental conditions. Until relatively recently, insect ecologists have focused on the evolutionary significance of insect life histories and interactions with other species, especially as pollinators, herbivores, and predators (Price 1997). This focus has yielded much valuable information about the ecology of individual species and species associations and provides the basis for pest management or recovery of threatened and endangered species. However, relatively little attention has been given to the important role of insects as ecosystem engineers, other than to their effects on vegetation (especially commercial crop) or animal (especially human and livestock) dynamics.

Ecosystem ecology has advanced rapidly during the past 50 years. Major strides have been made in understanding how species interactions and environmental conditions affect rates of energy and nutrient fluxes in different types of ecosystems, how these provide free services (such as air and water filtration), and how environmental conditions both affect and reflect community structure (e.g., Costanza *et al.* 1997, Daily 1997, H. Odum 1996). Interpreting the responses of a diverse community to multiple interacting environmental factors in integrated ecosystems requires new approaches, such as multivariate statistical analysis and modeling (e.g., Gutierrez 1996, Liebhold *et al.* 1993, Marcot *et al.* 2001, Parton *et al.* 1993). Such approaches may involve loss of detail, such as combination of species into phylogenetic or functional groupings. However, an ecosystem approach provides a framework for integrating insect ecology with the changing patterns of ecosystem structure and function and for applying insect ecology to understanding of ecosystem, landscape, and global issues, such as climate change or sustainability of ecosystem resources. Unfortunately, few ecosystem studies have involved insect ecologists and, therefore, have tended to underrepresent insect responses and contributions to ecosystem changes.

I. SCOPE OF INSECT ECOLOGY

Insect ecology is the study of interactions between insects and their environment. Ecology is, by its nature, integrative, requiring the contributions of biologists, chemists, geologists, climatologists, soil scientists, geographers, mathematicians, and others to understand how the environment affects organisms, populations, and communities and is affected by their activities through a variety of feedback loops (Fig. 1.2). Insect ecology has both basic and applied goals. Basic goals are to understand and model these interactions and feedbacks (e.g., Price 1997). Applied goals are to evaluate the extent to which insect responses to environmental changes, including those resulting from anthropogenic activities, mitigate or exacerbate ecosystem change (e.g., Croft and Gutierrez 1991, Kogan 1998), especially in managed ecosystems.

Research on insects and associated arthropods (e.g., spiders, mites, centipedes, millipedes, crustaceans) has been critical to development of the fundamental principles of ecology, such as evolution of social organization (Haldane 1932, Hamilton 1964, E. Wilson 1973); population dynamics (Coulson 1979, Morris 1969, Nicholson 1958, Varley and Gradwell 1970, Varley *et al.* 1973, Wellington *et al.* 1975); competition (Park 1948, 1954); predator–prey interaction (Nicholson and Bailey 1935); mutualism (Batra 1966, Bronstein 1998, Janzen 1966, Morgan 1968, Rickson 1971, 1977); island biogeography (Darlington 1943, MacArthur and Wilson 1967, Simberloff 1969, 1978); metapopulation ecology (Hanski 1989); and regulation of ecosystem processes, such as primary productivity, nutrient cycling, and succession (Mattson and Addy 1975, J. Moore *et al.* 1988, Schowalter 1981, Seastedt 1984). Insects and other arthropods are small and

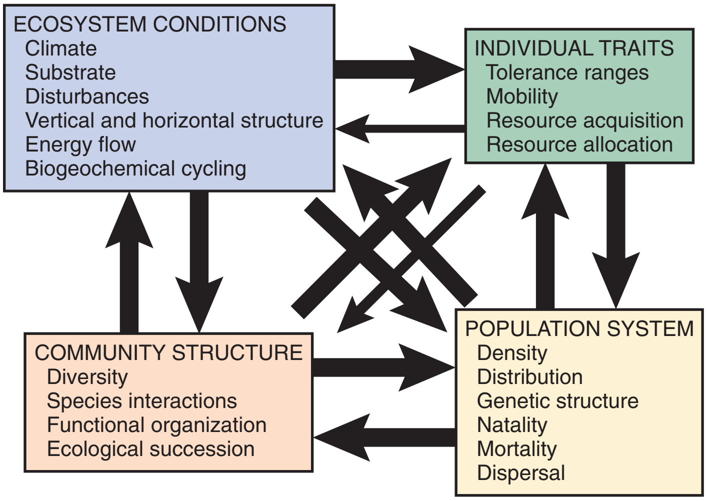


FIG. 1.2 Diagrammatic representation of feedbacks between various levels of ecological organization. Size of arrows is proportional to strength of interaction. Note that individual traits have a declining direct effect on higher organizational levels but are affected strongly by feedback from all higher levels.

easily manipulated subjects. Their rapid numeric responses to environmental changes facilitate statistical discrimination of responses and make them particularly useful models for experimental study. Insects also have been recognized for their capacity to engineer ecosystem change, making them ecologically and economically important.

Insects fill a variety of important ecological (functional) roles. Many species are key pollinators. Pollinators and plants have adapted a variety of mechanisms for ensuring transfer of pollen, especially in tropical ecosystems where sparse distributions of many plant species require a high degree of pollinator fidelity to ensure pollination among conspecific plants (Feinsinger 1983). Other species are important agents for dispersal of plant seeds, fungal spores, bacteria, viruses, or other invertebrates (Moser 1985, Nault and Ammar 1989, Sallabanks and Courtney 1992). Herbivorous species are particularly well-known as agricultural and forestry "pests," but their ecological roles are far more complex, often stimulating plant growth, affecting nutrient fluxes, or altering the rate and direction of ecological succession (MacMahon 1981, Maschinski and Whitham 1989, Mattson and Addy 1975, Schowalter and Lowman 1999, Schowalter *et al.* 1986, Trumble *et al.* 1993). Insects and associated arthropods are instrumental in processing of organic detritus in terrestrial and aquatic ecosystems and influence soil fertility and water quality (Kitchell *et al.* 1979, Seastedt and Crossley 1984). Woody litter decomposition usually is delayed until insects penetrate the bark barrier and inoculate the wood with saprophytic fungi and other microorganisms (Ausmus 1977, Dowding 1984, Swift 1977). Insects are important resources for a variety of fish, amphibians, reptiles, birds, and mammals, as well as for other invertebrate predators and parasites. In addition, some insects are important vectors of plant and animal diseases, including diseases such as malaria and plague, that have affected human and wildlife population dynamics.

The significant economic and medical or veterinary importance of many insect species is the reason for distinct entomology programs in various universities and government agencies. Damage to agricultural crops and transmission of human and livestock diseases has stimulated interest in, and support for, study of factors influencing abundance and effects of these insect species. Much of this research has focused on evolution of life history strategies, interaction with host plant chemistry, and predator–prey interactions as these contribute to our understanding of "pest" population dynamics, especially population regulation by biotic and abiotic factors. However, failure to understand these aspects of insect ecology within an ecosystem context undermines our ability to predict and manage insect populations and ecosystem resources effectively (Kogan 1998). Suppression efforts may be counterproductive to the extent that insect outbreaks represent ecosystem-level regulation of critical processes in some ecosystems.

II. ECOSYSTEM ECOLOGY

The ecosystem is a fundamental unit of ecological organization, although its boundaries are not easily defined. An ecosystem generally is considered to represent the integration of a more or less discrete community of organisms and the abiotic conditions at a site (Fig. 1.3). However, research and environmental policy decisions are recognizing the importance of scale in ecosystem studies (i.e., extending research or extrapolating results to landscape, regional, and even global scales; e.g., Holling 1992, G. Turner 1989). Ecosystems are interconnected, just as the species within them are interconnected. Exports from one ecosystem become imports for others. Energy, water, organic matter, and nutrients from terrestrial ecosystems are major sources of these resources for many aquatic ecosystems. Organic matter and nutrients eroded by wind from arid ecosystems are filtered from the airstream by ecosystems downwind. Some ecosystems within a landscape or watershed are the sources of colonists for recently disturbed ecosystems. Insect outbreaks can spread from one ecosystem to another. Therefore, our perspective of the ecosystem needs to incorporate the concept of interactions among ecosystem types (patches) within the landscape or watershed.

Overlapping gradients in abiotic conditions establish the template that limits options for community development, but established communities can modify abiotic conditions to varying degrees. For example, minimum rates of water and nutrient supply are necessary for establishment of grasslands or forests, but once canopy cover and water and nutrient storage capacity in organic material have developed, the ecosystem is relatively buffered from changes in water and nutri-

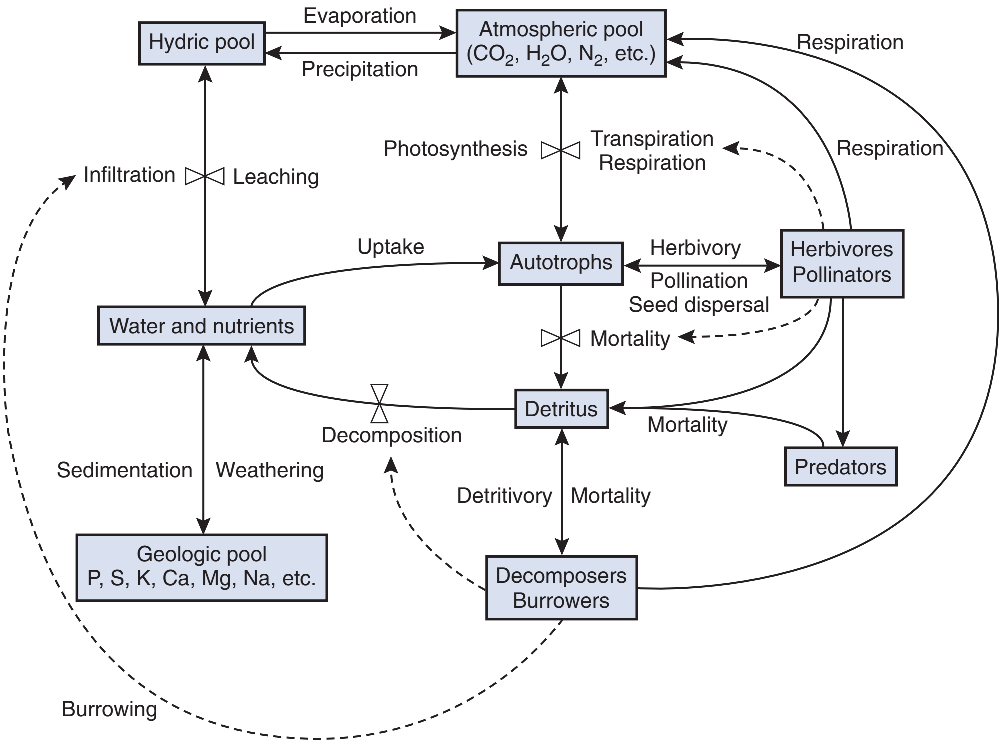


FIG. 1.3 Conceptual model of ecosystem structure and function. Boxes represent storage compartments, lines represent fluxes, and hourglasses represent regulation. Solid lines are direct transfers of energy and matter, and dashed lines are informational or regulatory pathways.

ent supply (e.g., E. Odum 1969, Webster *et al.* 1975). Although ecosystems usually are defined on the basis of the dominant vegetation (e.g., tundra, desert, marsh, grassland, forest) or type of water body (stream, pond, lake), characteristic insect assemblages also differ among ecosystems. For example, wood-boring insects (e.g., ambrosia beetles, wood wasps) are characteristic of communities in wooded ecosystems (shrub and forest ecosystems) but clearly could not survive in ecosystems lacking woody resources.

A. Ecosystem Complexity

Ecosystems are complex systems with structure, represented by abiotic resources and a diverse assemblage of component species and their products (such as organic detritus and tunnels) and function, represented by fluxes of energy and matter among biotic and abiotic components (see Fig. 1.3). This complexity extends to the spatial delineation of an ecosystem. Ecosystems can be identified at microcosm and mesocosm scales (e.g., decomposing logs or treehole pools), patch scale (area encompassing a particular community on the landscape), landscape scale (the mosaic of patch types representing different edaphic conditions or successional stages that compose a broader ecosystem type), and the regional or biome scale.

Addressing taxonomic, temporal, and spatial complexity has proved to be a daunting challenge to ecologists, who must decide how much complexity can be ignored safely (Gutierrez 1996, Polis 1991a, b). Evolutionary and ecosystem ecologists have taken contrasting approaches to dealing with this complexity in ecological studies. The evolutionary approach emphasizes adaptive aspects of life histories, population dynamics, and species interactions. This approach restricts complexity to interactions among one or a few species and their hosts, competitors, predators, or other biotic and abiotic environmental factors and often ignores the complex feedbacks at the ecosystem level. In contrast, the ecosystem approach emphasizes rates and directions of energy and matter fluxes. This approach restricts complexity to fluxes among functional groups and often ignores the contributions of individual species. Either approach, by itself, limits our ability to understand feedbacks among individual, population, community, and ecosystem parameters and to predict effects of a changing global environment on these feedbacks.

B. The Hierarchy of Subsystems

Complex systems with feedback mechanisms can be partitioned into component subsystems, which are themselves composed of sub-subsystems. Viewing the ecosystem as a nested hierarchy of subsystems (Table 1.1), each with its particular properties and processes (Coulson and Crossley 1987, Kogan 1998, O'Neill *et al.* 1986), facilitates understanding of complexity. Each level of the hierarchy can be studied at an appropriate level of detail, and its properties can be explained by the integration of its subsystems. For example, population responses to changing environmental conditions reflect the net physiological and behavioral

TABLE 1.1 Ecological hierarchy and the structural and functional properties characterizing each level.

Ecological level	Structure	Function
Global	Biome distribution, atmospheric condition, climate, sea level, total biomass	Gas, water, nutrient exchange between terrestrial and marine systems
Biome	Landscape pattern, temperature, moisture profile, integrated biomass of ecosystems	Energy and matter fluxes, disturbance regimen, migration
Landscape	Disturbance pattern, community distribution, metapopulation structure	Energy and matter fluxes, integrated NPP of ecosystems, colonization and extinction
Ecosystem	Vertical and horizontal structure, disturbance type and frequency, biomass, functional organization	Energy and matter fluxes, succession, NPP, herbivory, decomposition, pedogenesis
Community	Diversity, trophic organization	Species interactions, temporal and spatial changes
Population	Density, dispersion, age structure, genetic structure	Natality, mortality, dispersal, gene flow, temporal and spatial changes
Individual	Anatomy, genome	Physiology/learning/behavior, resource acquisition and allocation

NPP, net primary productivity.

responses of individuals that determine their survival and reproduction. Changes in community structure reflect the dynamics of component populations. Fluxes of energy and matter through the ecosystem reflect community organization and interaction. Landscape structure reflects ecosystem processes that affect movement of individuals. Hence, the integration of structure and function at each level determines properties at higher levels.

At the same time, the conditions produced at each level establish the context, or template, for responses at lower levels. Population structure resulting from individual survival, dispersal, and reproduction determines future survival, dispersal, and reproduction of individuals. Ecosystem conditions resulting from community interactions affect subsequent behavior of individual organisms, populations, and the community. Recognition of feedbacks from higher levels has led to developing concepts of inclusive fitness (fitness accruing through feedback from benefit to a group of organisms) and ecosystem self-regulation (see Chapter 15). The hypothesis that insects function as cybernetic regulators that stabilize ecosystem properties (M. Hunter 2001b, Mattson and Addy 1975, Schowalter

1981) has been one of the most important and controversial concepts to emerge from insect ecology.

Ecosystem processes represent the integration of processes at the level of component communities. Component communities are subsystems (i.e., more or less discrete assemblages of organisms based on particular resources). For example, the relatively distinct soil faunas associated with fungal, bacterial, or plant root resources represent different component communities (J. Moore and Hunt 1988). Component communities are composed of individual species populations, with varying strategies for acquiring and allocating resources. Species populations, in turn, are composed of individual organisms with variation in individual physiology and behavior. Ecosystems can be integrated at the landscape or biome levels, and biomes can be integrated at the global (biosphere) level. Spatial and temporal scales vary across this hierarchy. Whereas individual physiology and behavior operate on small scales of space and time (i.e., limited to the home range and life span of the individual), population dynamics span landscape and decadal scales, and ecosystem processes, such as patterns of resource turnover, recovery from disturbance, or contributions to atmospheric carbon, operate at scales from the patch to the biome and from decades to millenia.

Modeling approaches have greatly facilitated understanding of the complexity and consequences of interactions and linkages within and among these organizational levels of ecosystems. The most significant challenges to ecosystem modelers remain (1) the integration of appropriately detailed submodels at each level to improve prediction of causes and consequences of environmental changes and (2) the evaluation of contributions of various taxa (including particular insects) or functional groups to ecosystem structure and function. In particular, certain species or structures have effects disproportionate to their abundance or biomass. Studies focused on the most abundant or conspicuous species or structures fail to address substantial contributions of rare or inconspicuous components, such as many insects.

C. Regulation

An important aspect of this functional hierarchy is the "emergence" of properties that are not easily predictable by simply adding the contributions of constitutive components. Emergent properties include feedback processes at each level of the hierarchy. For example, individual organisms acquire and allocate energy and biochemical resources, affecting resource availability and population structure in ways that change the environment and determine future options for acquisition and allocation of these resources. Regulation of density and resource use emerges at the population level through negative feedback (from declining resource availability and increasing predation at larger population sizes), which functions to prevent overexploitation, or through positive feedback, which prevents extinction. Similarly, species populations acquire and transport resources, but regulation of energy flow and biogeochemical cycling emerge at the ecosystem level. Potential regulation of atmospheric and oceanic pools of carbon and nutrients at the global level reflects integration of biogeochemical cycling and energy fluxes among the Earth's ecosystems.

Information flow and feedback processes are the mechanisms of regulation. Although much research has addressed energy and material flow through food webs, relatively little research has quantified the importance of indirect interactions or information flow. Indirect interactions and feedbacks are common features of ecosystems. For example, herbivores feeding above-ground alter the availability of resources for root-feeding organisms (Gehring and Whitham 1991, 1995, Masters *et al.* 1993); early-season herbivory can affect plant suitability for later-season herbivores (Harrison and Karban 1986, M. Hunter 1987). Information can be transmitted as volatile compounds that advertise the location and physiological condition of prey, the proximity of potential mates, and the population status of predators. Such information exchange is critical to discovery of suitable hosts, attraction of mates, regulation of population density, and defense against predators by many (if not all) insects.

This ecosystem information network among the members of the community, along with resource supply and demand relationships, provides the basis for regulation of ecosystem processes. Levels of herbivory and predation are sensitive to resource availability. If environmental conditions increase resource abundance at any trophic level, communication to, and response by, the next trophic level provides negative feedback that reduces resource abundance. Negative feedback is a primary mechanism for stabilizing population sizes, species interactions, and process rates in ecosystems. Some interactions provide positive feedback, such as cooperation or mutualism. Although positive feedback is potentially destabilizing, it may reduce the probability of population decline to extinction. The apparent ability of many ecosystems to reduce variation in structure and function suggests that ecosystems are self-regulating (i.e., they behave like cybernetic systems; e.g., E. Odum 1969, Patten and Odum 1981). Insects could be viewed as important mechanisms of regulation because their normally small biomass requires relatively little energy or matter to maintain, and their rapid and dramatic population response to environmental changes constitutes an effective and efficient means for reducing deviation in nominal ecosystem structure and function. This developing concept of ecosystem self-regulation has major implications for ecosystem responses to anthropogenic change in environmental conditions and for our approaches to managing insects and ecosystem resources.

III. ENVIRONMENTAL CHANGE AND DISTURBANCE

Environmental changes across temporal and spatial gradients are critical components of an ecosystem approach to insect ecology. Insects are highly responsive to environmental changes, including those resulting from anthropogenic activity. Many insects have considerable capacity for long distance dispersal, enabling them to find and colonize isolated resources as these appear. Other insects are flightless and vulnerable to environmental change or habitat fragmentation. Because of their small size, short life spans, and high reproductive rates, abundances of many species can change several orders of magnitude on a seasonal or annual time scale, minimizing time lags between environmental changes and population adjustment to new conditions. Such changes are easily detectable and make insects more useful as indicators of environmental changes than are larger or longer-lived organisms. In turn, insect responses to environmental change can affect ecosystem patterns and processes dramatically. Some phytophagous species are well-known for their ability, at high population levels, to reduce host plant density and productivity greatly over large areas. Effects of other species may be more subtle but equally significant from the standpoint of long-term ecosystem structure and function.

Environmental change operates on a continuum of spatial and temporal scales. Although strict definitions of environmental change and disturbance have proved problematic, environmental change generally occurs over a longer term, whereas disturbances are short-term events (Walker and Willig 1999, P. White and Pickett 1985). Chronic changes in temperature or precipitation patterns, such as following the last glaciation, occur on a scale of 10^3–10^5 years and may be barely detectable on human time scales. Long-term changes may be difficult to distinguish from cycles operating over decades or centuries, leading to disagreements over whether measured changes represent a fluctuation or a long-term trend. Acute events, such as fires or storms, are more recognizable as disturbances that have dramatic effects on time scales of seconds to hours. However, the duration at which a severe drought, for example, is considered a climate change, rather than a disturbance, has not been determined. The combination of climate and geologic patterns, disturbances, and environmental changes creates a constantly shifting landscape mosaic of various habitat and resource patches that determine where and how insects and other organisms find suitable conditions and resources.

Insect outbreaks traditionally have been viewed as disturbances (P. White and Pickett 1985, Walker and Willig 1999). P. White and Pickett (1985) proposed that disturbance be defined as any relatively discrete event in time that causes measurable change in population, community, or ecosystem structure or function. This definition clearly incorporates insect outbreaks. Similarly, human activities have become increasingly prominent agents of disturbance and environmental change.

Insect outbreaks are comparable to physical disturbances in terms of severity, frequency, and scale. Insects can defoliate or kill most host plants over large areas, up to 10^3–10^6 ha (e.g., Furniss and Carolin 1977). For example, 39% of a montane forest landscape in Colorado has been affected by insect outbreaks (spruce beetle, *Dendroctonus rufipennis)* since about 1633, compared to 59% by fire and 9% by snow avalanches (Veblen *et al.* 1994), with an average return interval of 117 years, compared to 202 years for fire. Frequent, especially cyclic, outbreaks of herbivorous insects probably have been important in selection for plant defenses.

However, unlike abiotic disturbances, insect outbreaks are biotic responses to a change in environmental conditions. Recent outbreaks most commonly reflect anthropogenic redistribution of resources, especially increased density of commercially valuable (often exotic) plant species. Outbreaks usually develop in dense patches of host plants and function to reduce host density, increase vegetation diversity, and increase water and nutrient availability (Schowalter *et al.* 1986). Management responses to insect outbreaks often are more damaging to ecosystem conditions than is the insect outbreak. For example, insecticides, such as arsenicals and chlorinated hydrocarbons, had long-term, nonselective effects on nontarget organisms. Removing dead or dying host plants, and even living plants, in advance of insect colonization has caused serious soil disturbance and erosion, as well as change in community structure. Principles of integrated pest management (IPM) improved approaches to managing insects by emphasizing adherence to ecological principles. Consideration of insects as integral components of potentially self-maintaining ecosystems could further improve our management of insects and ecosystem resources, within the context of global change.

Currently, human alteration of Earth's ecosystems is substantial and accelerating (J. Thomas *et al.* 2004, Vitousek *et al.* 1997). Anthropogenic changes to the global environment affect insects in various ways. Combustion of fossil fuels has elevated atmospheric concentrations of CO_2 (Beedlow *et al.* 2004, Keeling *et al.* 1995), methane, ozone, nitrous oxides, and sulfur dioxide, leading to increasingly acidic precipitation and prospects of global warming. Some insect species show high mortality as a direct result of atmospheric toxins, whereas other species are affected indirectly by changes in resource conditions induced by atmospheric change (Alstad *et al.* 1982, Arnone *et al.* 1995, Heliövaara 1986, Kinney *et al.* 1997, Lincoln *et al.* 1993, W. Smith 1981). A thinning ozone layer at higher altitudes and toxic ozone levels at lower altitudes have similar effects (Alstad *et al.* 1982). However, the anthropogenic changes with the most immediate effects are land-use patterns and redistribution of exotic species, including plants, insects, and livestock. These activities are altering and isolating natural communities at an unprecedented rate, leading to outbreaks of insect "pests" in crop monocultures and fragmented ecosystems (Roland 1993) and potentially threatening species incapable of surviving in increasingly inhospitable landscapes (Samways *et al.* 1996, Shure and Phillips 1991, A. Suarez *et al.* 1998). J. Thomas *et al.* (2004) compared species losses of British butterflies, birds, and plants and found that loss of butterfly species has been greater than that of birds and plants; current rates of species disappearance represent the sixth major extinction event through time. Predicting and mitigating species losses or pest outbreaks depends strongly on our understanding of insect ecology within the context of ecosystem structure and function.

IV. ECOSYSTEM APPROACH TO INSECT ECOLOGY

Insect ecology can be approached using a hierarchical model (Coulson and Crossley 1987). Ecosystem conditions represent the environment (i.e., the combination of physical conditions, interacting species, and availability of resources) that determine survival and reproduction by individual insects, but in turn, insect activities alter vegetation cover, soil properties, community organization, etc. (see Fig. 1.2). A hierarchical approach offers a means of integrating evolutionary and ecosystem approaches to studying insect ecology. The evolutionary approach focuses at lower levels of resolution (individual, population, community) and offers explanation (i.e., natural selection) for individual and population adaptation to environmental conditions. Such explanation is critical to understanding how organisms respond to environmental change. At the same time, natural selection represents feedback from ecosystem conditions as these are altered by the activities of co-evolving organisms. The evolutionary and ecosystem perspectives are most complementary at the community level, where species diversity emphasized by the evolutionary approach is the basis for functional organization emphasized by the ecosystem approach.

Although the evolutionary approach has provided valuable explanations for how complex interactions have arisen, current environmental issues require an understanding of how insect functional roles affect ecosystem, landscape, and global processes. Insect ecologists have recognized insects as important components of ecosystems but have only begun to explore the key roles insects play as integral components of ecosystems. Insects affect primary productivity and organic matter turnover in ways that greatly alter, and potentially regulate, ecological succession, biogeochemical cycling, carbon and energy flux, albedo, and hydrology, perhaps affecting regional and global climate as well. These roles may complement or exacerbate changes associated with human activities. Therefore, the purpose of this book is to address the fundamental issues of insect ecology as they relate to ecosystem, landscape, and global processes.

V. SCOPE OF THIS BOOK

This book is organized hierarchically to emphasize feedbacks among individual, population, and community levels and the ecosystems they represent. Four questions have been used to develop this text:

1. How do insects respond to variation in environmental conditions, especially gradients in abiotic factors and resource availability?
2. How do interactions among individuals affect the structure and function of populations and communities?
3. How do insect-induced changes in ecosystem properties affect the gradients in environmental conditions to which individuals respond?
4. How can this information be incorporated into management decisions and environmental policy?

Chapter and topic organization are intended to address these questions by emphasizing key spatial and temporal patterns and processes at each level and their integration among levels. Environmental policy and management decisions (Section V) depend on evaluation of insect effects on ecosystem parameters and their responses to environmental change. The evaluation of insect effects on ecosystem parameters and their responses to environmental change (Section IV) depends on understanding of species diversity, interactions, and community organization (Section III) that, in turn, depends on understanding of population dynamics and biogeography (Section II), that depends on understanding of individual physiological and behavioral responses to environmental variation (Section I).

Three themes integrate these ecological levels. First, spatial and temporal patterns of environmental variability and disturbance determine survival and reproduction of individuals and patterns of population, community, and ecosystem structure and dynamics. Individual acquisition and allocation of resources, population distribution and colonization and extinction rates, community patterns and successional processes, and ecosystem structure and function reflect environmental conditions. Second, energy and nutrients move through individuals, populations and communities, and abiotic pools. The net foraging success and resource use by individuals determines energy and nutrient fluxes at the population level. Trophic interactions among populations determine energy and nutrient fluxes at the community and ecosystem levels. Third, regulatory mechanisms at each level serve to balance resource demands with resource availability (carrying capacity) or to dampen responses to environmental changes. Regulation results from a balance between negative feedback that reduces population size or process rates and positive feedback that increases population size or process rates. Regulation of population sizes and process rates tends to stabilize ecosystem conditions within ranges favorable to most members. The capacity to regulate environmental conditions increases from individual to ecosystem levels (see Fig. 1.2). If feedbacks within or among levels contribute to ecosystem stability, then human influences on ecosystem structure and function could enhance or seriously impair this function.

Section I (Chapters 2–4) addresses the physiological and behavioral ecology of insects. Physiology and behavior represent the means by which organisms interact with their environment. Physiology represents “fixed” adaptations to predictable variation in environmental conditions, whereas behavior represents a more flexible means of adjusting to unpredictable variation. Chapter 2 summarizes insect responses to variable habitat conditions, especially gradients in climate, water, and chemical conditions. Chapter 3 describes physiological and behavioral mechanisms for acquiring energy and matter resources, and Chapter 4 addresses the allocation of assimilated resources to various metabolic and behavioral pathways. These chapters provide a basis for understanding distribution patterns and movement of energy and matter through populations and communities.

Section II (Chapters 5–7) deals with population ecology. Populations of organisms integrate variation in adaptive strategies and foraging patterns among individuals. Chapter 5 outlines population systems, including population structure and the processes of reproduction, mortality, and dispersal. Chapter 6 addresses processes and models of population change; Chapter 7 describes biogeography, processes and models of colonization and extinction, and metapopulation dynamics over landscapes. These population parameters determine population effects on ecological processes through time in various patches across regional landscapes.

Section III (Chapters 8–10) addresses community ecology. Species populations interact with other species in a variety of ways that determine changes in community structure through time and space. Chapter 8 describes species interactions (e.g., competition, predation, symbioses). Chapter 9 addresses measures of diversity and community structure and spatial patterns in community structure. Chapter 10 addresses changes in community structure over time, especially community responses to environmental change. These community characteristics determine spatial and temporal patterns of energy and nutrient storage and flux through ecosystems.

Section IV (Chapters 11–15) focuses on ecosystems and is the unique contribution of this text to graduate education in insect ecology. Chapter 11 addresses general aspects of ecosystem structure and function, especially processes of energy and matter storage and flux that determine resource availability. Chapter 12 describes patterns of herbivory and effects on ecosystem parameters; Chapter 13 describes patterns and effects of pollination, seed predation, and seed dispersal; and Chapter 14 describes patterns and effects of detritivory and burrowing on ecosystem processes. Chapter 15 addresses the developing concept of ecosystem self-regulation and mechanisms, including species diversity and insect effects, that may contribute to ecosystem stability.

Section V (Chapter 16) provides synthesis and application. Chapter 16 summarizes and synthesizes major concepts. This chapter also provides examples of applications and suggests future directions and data necessary to improve understanding of linkages and feedbacks among hierarchical levels. Solutions to environmental problems require consideration of insect ecology at ecosystem, landscape, and global levels. Although the focus of this book clearly is on insects, examples from studies of other organisms are used where appropriate to illustrate concepts.

SECTION I

ECOLOGY OF INDIVIDUAL INSECTS

THE INDIVIDUAL ORGANISM IS A FUNDAMENTAL unit of ecology. Organisms interact with their environment and affect ecosystem processes largely through their cumulative physiological and behavioral responses to environmental variation. Individual success in finding and using necessary habitats and resources to gain reproductive advantage determines fitness. Insects have a number of general attributes that have contributed to their ecological success (Romoser and Stoffolano 1998).

First, small size (an attribute shared with other invertebrates and microorganisms) has permitted exploitation of habitat and food resources at a microscopic scale. Insects can take shelter from adverse conditions in microsites too small for larger organisms (e.g., within individual leaves). Large numbers of insects can exploit the resources represented by a single leaf, often by partitioning leaf resources. Some species feed on cell contents, others on sap in leaf veins, some on top of the leaf, others on the underside, and some internally. At the same time, small size makes insects sensitive to changes in temperature, moisture, air or water chemistry, and other factors.

Second, the exoskeleton (shared with other arthropods) provides protection against predation and desiccation or water-logging (necessary for small organisms) and innumerable points of muscle attachment (for flexibility). However, the exoskeleton also limits the size attainable by arthropods. The increased weight of exoskeleton required to support larger body size would limit mobility. Larger arthropods occurred prehistorically, before the appearance of faster, more flexible vertebrate predators. Larger arthropods also occur in aquatic environments, where water helps support their weight.

Third, metamorphosis is necessary for (exoskeleton-limited) growth but permits partitioning of habitats and resources among life stages. Immature and adult insects can differ dramatically in form and function and thereby live in different habitats and feed on different resources, reducing intraspecific competition. For example, dragonflies and mayflies live in aquatic ecosystems during immature stages but in terrestrial ecosystems as adults. Many Lepidoptera feed on foliage as immatures and on nectar as adults. Among holometabolous insects, the quiescent, pupal stage facilitates survival during unfavorable environmental conditions. However, insects, as well as other arthropods, are particularly vulnerable to desiccation and predation during ecdysis (molting).

Finally, flight evolved first among insects and conferred a distinct advantage over other organisms. Flight permits rapid long-distance movement that facilitates discovery of new resources, as well as escape from predators or unfavorable conditions. Flight remains a dominant feature of insect ecology.

This section focuses on aspects of physiology and behavior that affect insect interactions with environmental conditions, specifically adaptations that favor survival and reproduction in variable environments and mechanisms for finding, exploiting, and allocating resources. Physiology and behavior are closely integrated. For example, movement, including dispersal, is affected by physiological perception of chemical gradients, fat storage, rapid oxygen supply, etc. Similarly, physiological processes are affected by insect selection of thermally suitable location, choice of food resources, etc. Chemical defenses against predators are based on physiological processes but often are enhanced by behaviors that facilitate expression of chemical defenses (e.g., thrashing or regurgitation). Organisms affect ecosystem processes, such as energy and nutrient fluxes, through their spatial and temporal patterns of energy and nutrient acquisition and allocation.

Chapter 2 deals with physiological and behavioral responses to changing environmental conditions. Chapter 3 addresses physiological and behavioral mechanisms for finding and exploiting resources. Chapter 4 describes allocation of resources to various metabolic pathways and behaviors that facilitate resource acquisition, mate selection, reproduction, interaction with other organisms, etc. Physiology and behavior interact to determine the conditions under which insects can survive and the means by which they acquire and use available resources. These ecological attributes affect population ecology (such as population structure, responses to environmental change and disturbances, biogeography, etc., Section II), community attributes (such as use of, or use by, other organisms as resources, Section III), and ecosystem attributes (such as rates and directions of energy and matter flows, Section IV).

2

Responses to Abiotic Conditions

INSECTS ARE A DOMINANT GROUP OF ORGANISMS IN VIRTUALLY ALL terrestrial, freshwater, and near-coastal marine habitats, including many of the harshest ecosystems on the globe (e.g., deserts, hot springs, and tundra). However, particular species have restricted ranges of occurrence dictated by their tolerances to a variety of environmental factors.

One of the earliest (and still important) objectives of ecologists was explanation of the spatial patterns of species distributions (e.g., Andrewartha and Birch 1954, A. Wallace 1876). The geographic ranges of insect species generally are determined by their tolerances, or the tolerances of their food resources and predators, to variation in abiotic conditions. Insect morphological, physiological, and behavioral adaptations reflect the characteristic physical conditions of the habitats in which they occur. However, variation in physical conditions requires some flexibility in physiological and behavioral traits. All ecosystems experience climatic fluctuation and periodic disturbances that affect the survival of organisms in the community. Furthermore, anthropogenic changes in habitat conditions increase the range of conditions to which organisms must respond.

I. THE PHYSICAL TEMPLATE

A. Biomes

Global patterns of temperature and precipitation, reflecting the interaction among latitude, global atmospheric and oceanic circulation patterns, and topography, establish a regional template of physical conditions that support characteristic communities, called "biomes" (Fig. 2.1) (Finch and Trewartha 1949). Latitudinal gradients in temperature from Earth's equator to its poles define the tropical, subtropical, temperate, and arctic zones. Precipitation patterns overlay these temperature gradients. Warm, humid air rises in the tropics, drawing air from higher latitudes into this equatorial convergence zone. The rising air cools and condenses moisture, resulting in a band of high precipitation and tropical rainforests centered on the equator. The cooled, dried air flows away from the equatorial zone and warms as it descends in the "horse latitudes," centered around 30 degrees N and S. These latitudes are dominated by arid grassland and desert ecosystems because of high evaporation rates in warm, dry air. Airflow at these latitudes diverges to the equatorial convergence zone and to similar convergence zones at about 60 degrees N and S latitudes. Rising air at 60 degrees N and S latitudes creates bands of relatively high precipitation and low temperature that support boreal forests. These latitudinal gradients in climate restrict the distribution of organisms on the basis of their tolerance ranges for temperature and moisture. No individual species is capable of tolerating the entire range of tropical to arctic temperatures or desert to mesic moisture conditions.

Mountain ranges interact with oceanic and atmospheric circulation patterns to modify latitudinal patterns of temperature, and precipitation. Mountains force airflow upward, causing cooling, condensation, and precipitation on the windward side (Fig. 2.2). Drier air descends on the leeward side where it gains moisture through evaporation. This orographic effect leads to development of mesic environments on the windward side and arid environments on the leeward side of mountain ranges. Mountains are characterized by elevational gradients of temperature, moisture, and atmospheric conditions (e.g., lower elevations tend to be warmer and drier, whereas higher elevations are cooler and moister). Concentrations of oxygen and other gases decline with elevation so that species occurring at higher elevations must be capable of surviving at low gas concentrations. The montane gradient is much shorter than the corresponding latitudinal gradient, with the same temperature change occurring in a 1000-m difference in elevation or an 880-km difference in latitude. Hence, the range of habitat conditions that occur over a wide latitudinal gradient occurs on a smaller scale in montane areas.

The relatively distinct combinations of temperature and precipitation (MacMahon 1981) determine the assemblage of species capable of surviving and defining the characteristic community type (i.e., tundra, temperate deciduous forest, temperate coniferous forest, tropical rainforest, tropical dry forest, grassland, savanna, chaparral, and desert; Fig. 2.3). Representative terrestrial biomes and their seasonal patterns of temperature and precipitation are shown in Figs. 2.4 and 2.5.

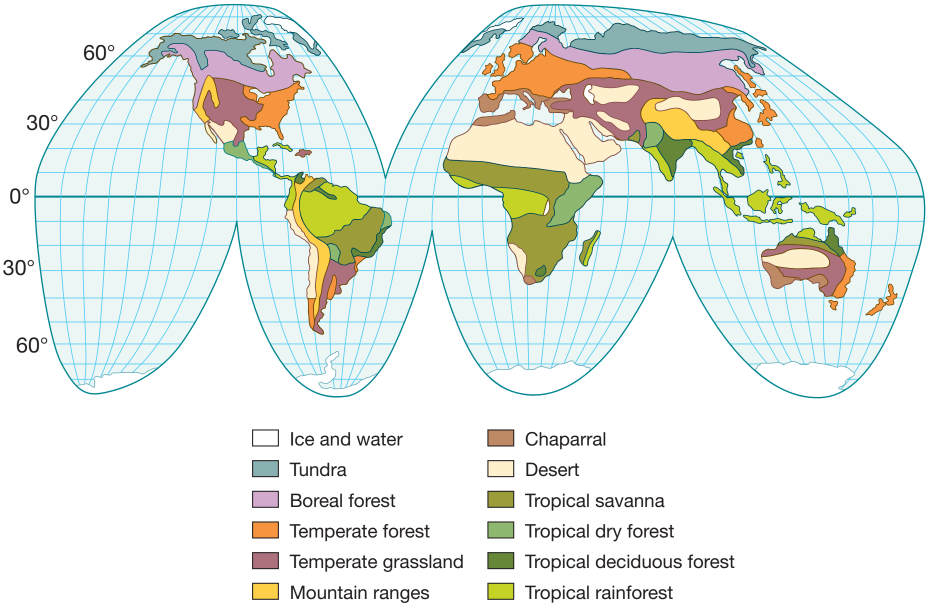


FIG. 2.1 Global distribution of the major terrestrial biomes. The distribution of biomes is affected by latitude, global atmospheric and oceanic circulation patterns, and major mountain ranges. Modified from Finch and Trewartha (1949) with permission from McGraw-Hill and E. Odum (1971) with permission from Saunders College Publishing.

Habitat conditions in terrestrial biomes are influenced further by topographic relief, substrate structure and chemistry, and exposure to wind. For example, topographic relief creates gradients in solar exposure and soil drainage, as well as in temperature and moisture, providing local habitats for unique communities. Local differences in substrate structure and chemistry may limit the ability of many species of plants and animals, characteristic of the surrounding biome, to survive. Some soils (e.g., sandy loams) are more fertile or more conducive to excavation than others; serpentine soils and basalt flows require special adaptations for survival by plants and animals. Insects that live in windy areas, especially alpine tundra and oceanic islands, often are flightless as a result of selection against individuals blown away in flight. The resulting isolation of populations results in rapid speciation.

Aquatic biomes are formed by topographic depressions and gradients that create zones of standing or flowing water. Aquatic biomes vary in size, depth, flow rate, and marine influence (i.e., lakes, ponds, streams, rivers, estuaries, and tidal marshes; Fig. 2.6). Lotic habitats often show considerable gradation in temperature and solute concentrations with depth. Because water has high specific heat, water changes temperature slowly relative to air temperature. However, because water is most dense at 4°C, changes in density as temperature changes result in seasonal stratification of water temperature. Thermal stratification develops in the summer, as the surface of standing bodies of water warms and traps cooler, denser water below the thermocline (the zone of rapid temperature change), and

FIG. 2.2 Orographic effect of mountain ranges. Interruption of airflow and condensation of precipitation on the windward side (*right*) and clear sky on the leeward side (*left*) of Mt. Hood, Cascade Mountains, Oregon, United States. Please see extended permission list pg 569.

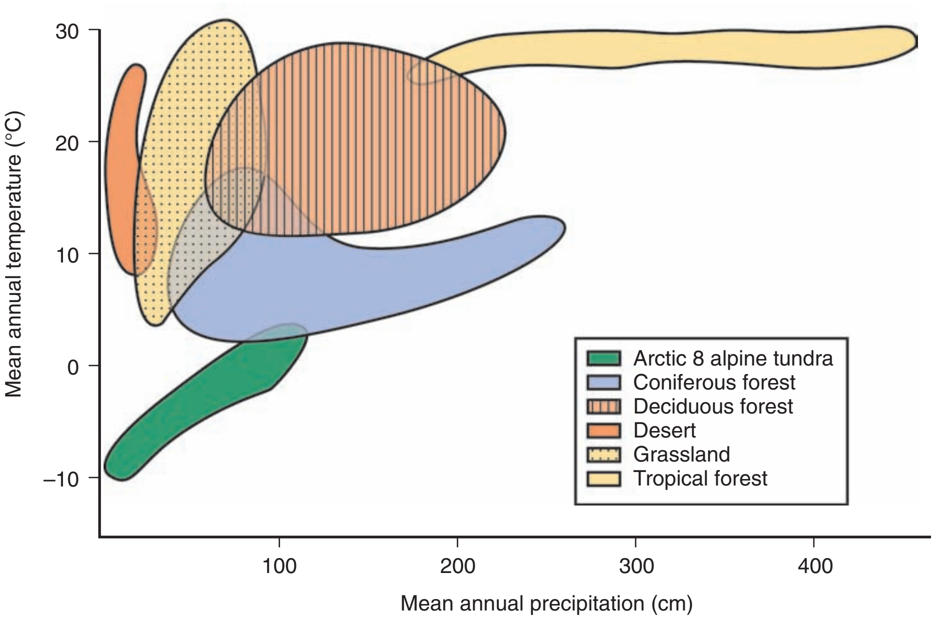


FIG. 2.3 Discrimination of geographic ranges of major terrestrial biomes on the basis of temperature and precipitation. From MacMahon (1981) with permission from Springer-Verlag. Please see extended permission list pg 569.

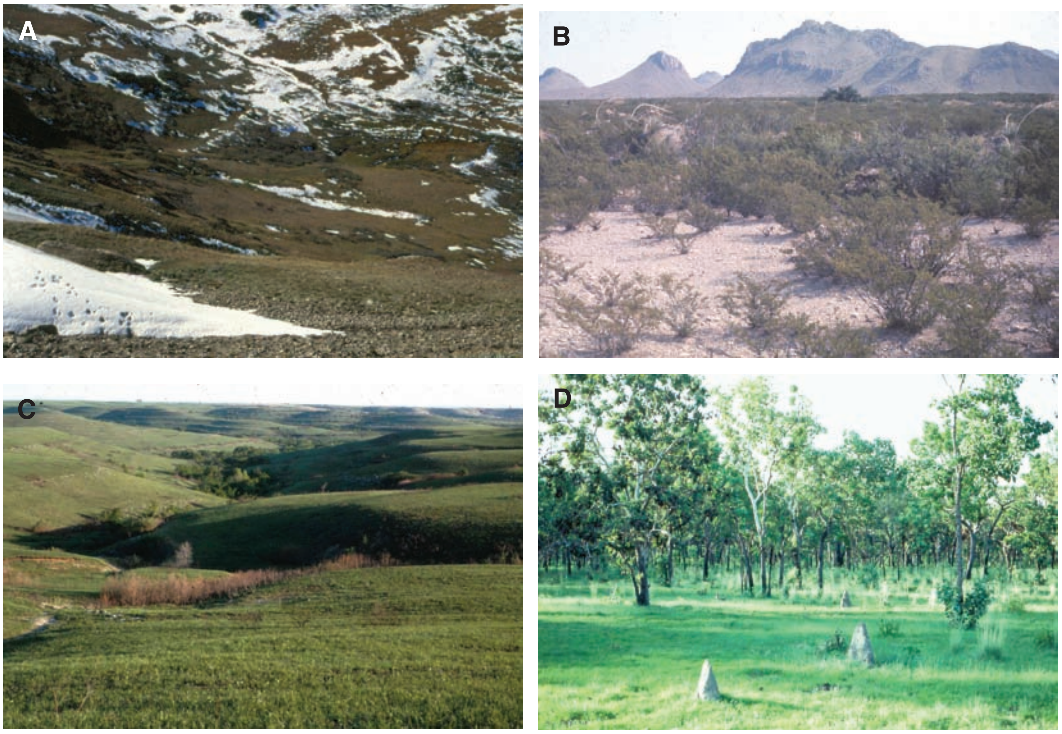


FIG. 2.4 Examples of ecosystem structure in representative terrestrial biomes. **A:** tundra (alpine) (western United States), **B:** desert shrubland (southwestern United States), **C:** grassland (central United States), **D:** tropical savanna (note termite mounds in foreground; northern Australia), **E:** boreal forest (northwestern United States), **F:** temperate deciduous forest (southeastern United States), and **G:** tropical rainforest (northern Panamá).

again in the winter, as freezing water rises to the surface, trapping warmer and denser water below the ice. During fall and spring, changing surface temperatures result in mixing of water layers and movement of oxygen and nutrients throughout the water column. Hence, deeper zones in aquatic habitats show relatively little variation in temperature, allowing aquatic insects to continue development and activity throughout the year, even in temperate regions.

Habitat conditions in aquatic biomes are influenced further by substrate structure and chemistry; amount and chemistry of regional precipitation; and the characteristics of surrounding terrestrial communities, including conditions upstream. Substrate structure and chemistry determine flow characteristics (including turbulence), pH, and inputs of nutrients from sedimentary sources. Amount and chemistry of regional precipitation determine regularity of water flow and inputs of atmospheric gases and nutrients. Characteristics of surrounding communities determine the degree of exposure to sunlight and the character and condition of allocthonus inputs of organic matter and sediments.

FIG. 2.4 (*Continued*)

B. Environmental Variation

Physical conditions vary seasonally in most biomes (see Fig. 2.5). Temperate ecosystems are characterized by obvious seasonality in temperature, with cooler winters and warmer summers, and also may show distinct seasonality in precipitation patterns, resulting from seasonal changes in the orientation of Earth's axis relative to the sun. Although tropical ecosystems experience relatively consistent temperatures, precipitation often shows pronounced seasonal variation (see Fig. 2.5). Aquatic habitats show seasonal variation in water level and circulation patterns related to seasonal patterns of precipitation and evaporation. Seasonal variation in circulation patterns can result in stratification of thermal layers and water chemistry in lotic systems. Intermittent streams and ponds may disappear during dry periods or when evapotranspiration exceeds precipitation.

Physical conditions also vary through time as a result of irregular events. Changes in global circulation patterns can affect biomes globally. For example, the east–west gradient in surface water temperature in the southern Pacific diminishes in some years, altering oceanic and atmospheric currents globally—the El Niño/southern oscillation (ENSO) phenomenon (Rasmussen and Wallace 1983, Windsor 1990). The effect of ENSO varies among regions. Particularly strong El Niño years (e.g., 1982–1983 and 1997–1998) are characterized by extreme drought conditions in some tropical ecosystems and severe storms and wetter conditions in some higher latitude ecosystems. Seasonal patterns of precipitation can be reversed (i.e., drier wet season and wetter dry season). The year following an El Niño year may show a rebound, an opposite but less intense, effect (La Niña). Windsor (1990) found a strong positive correlation between El Niño index and precipitation during the preceding year in Panamá. Precipitation in Panamá usually is lower than normal during El Niño years, in contrast to the greater precipitation accompanying El Niño in Peru and Ecuador (Windsor 1990, Zhou *et al*. 2002).

Many insects are sensitive to the changes in temperature and moisture that accompany such events. Stapp *et al*. (2004) found that local extinction of black-tailed prairie dog, *Cynomys ludovicianus*, colonies in the western Great Plains of North America was significantly greater during El Niño years as a result of flea-transmitted plague, *Yersinia pestis,* which spreads more rapidly during warmer, wetter conditions (Parmenter *et al*. 1999). Similarly, Zhou *et al*. (2002) reported that extremely high populations of sand flies, *Lutzomyia verrucarum,* were associated with El Niño conditions in Peru, resulting in near doubling of human cases of bartonellosis, an emerging, vectorborne, highly fatal infectious disease in the region (Fig. 2.7).

Solar activity, such as solar flares, may cause irregular departures from typical climatic conditions. Current changes in regional or global climatic conditions also may be the result of deforestation, desertification, fossil fuel combustion and other anthropogenic factors that affect albedo, global circulation patterns and atmospheric concentrations of CO_2, other greenhouse gases, and particulates. Characteristic ranges of tolerance to climatic factors determine the seasonal,

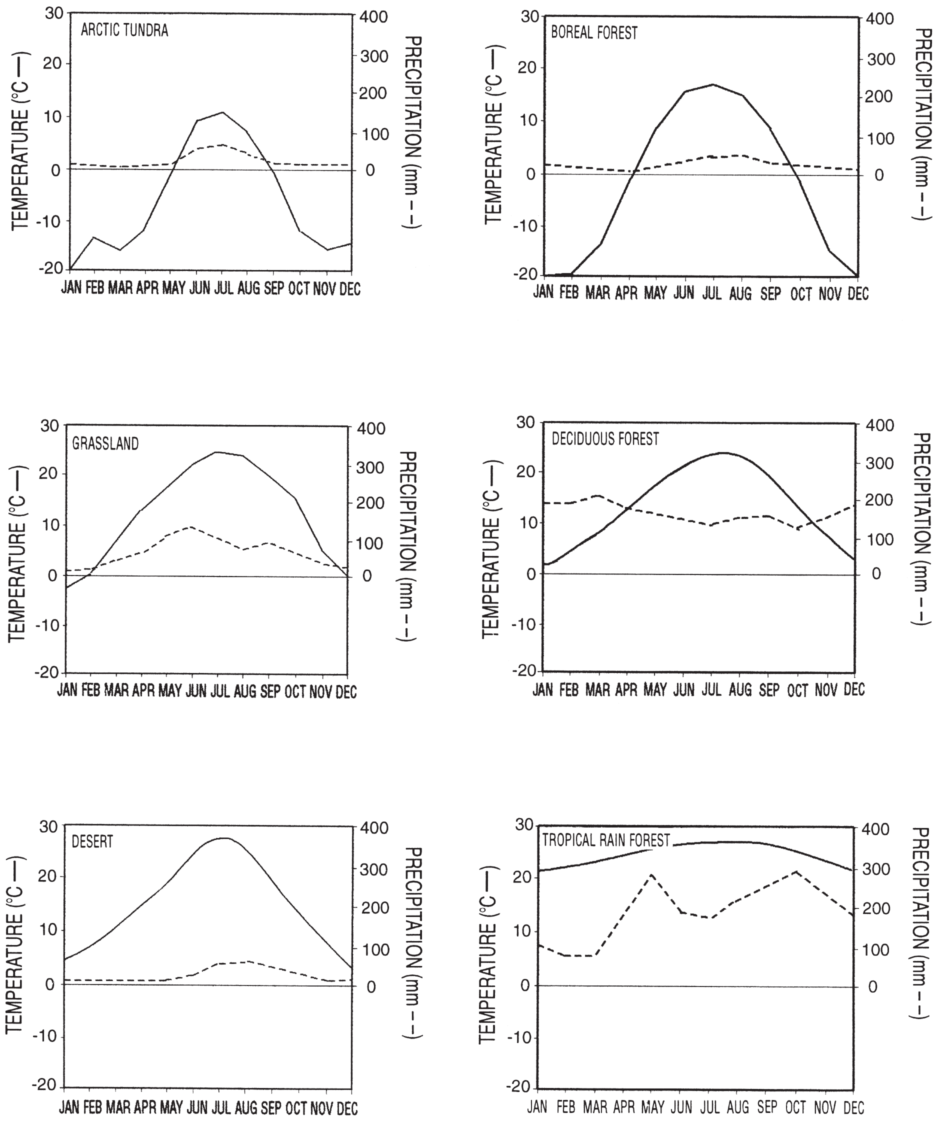


FIG. 2.5 Seasonal variation in temperature and precipitation at sites representing major biomes. Data from van Cleve and Martin (1991).

latitudinal, and elevational distributions of species and potential changes in distributions as a result of changing climate.

Terrestrial and aquatic biomes differ in the type and extent of variation in physical conditions. Terrestrial habitats are sensitive to changes in air temperature, wind speed, relative humidity, and other atmospheric conditions. Aquatic habitats are relatively buffered from sudden changes in air temperature but are sensitive to changes in flow rate, depth, and chemistry, especially changes in pH and concentrations of dissolved gases, nutrients, and pollutants. Vegetation cover insulates the soil surface and reduces albedo, thereby reducing diurnal and seasonal variation in soil and near-surface temperatures. Hence, desert biomes with

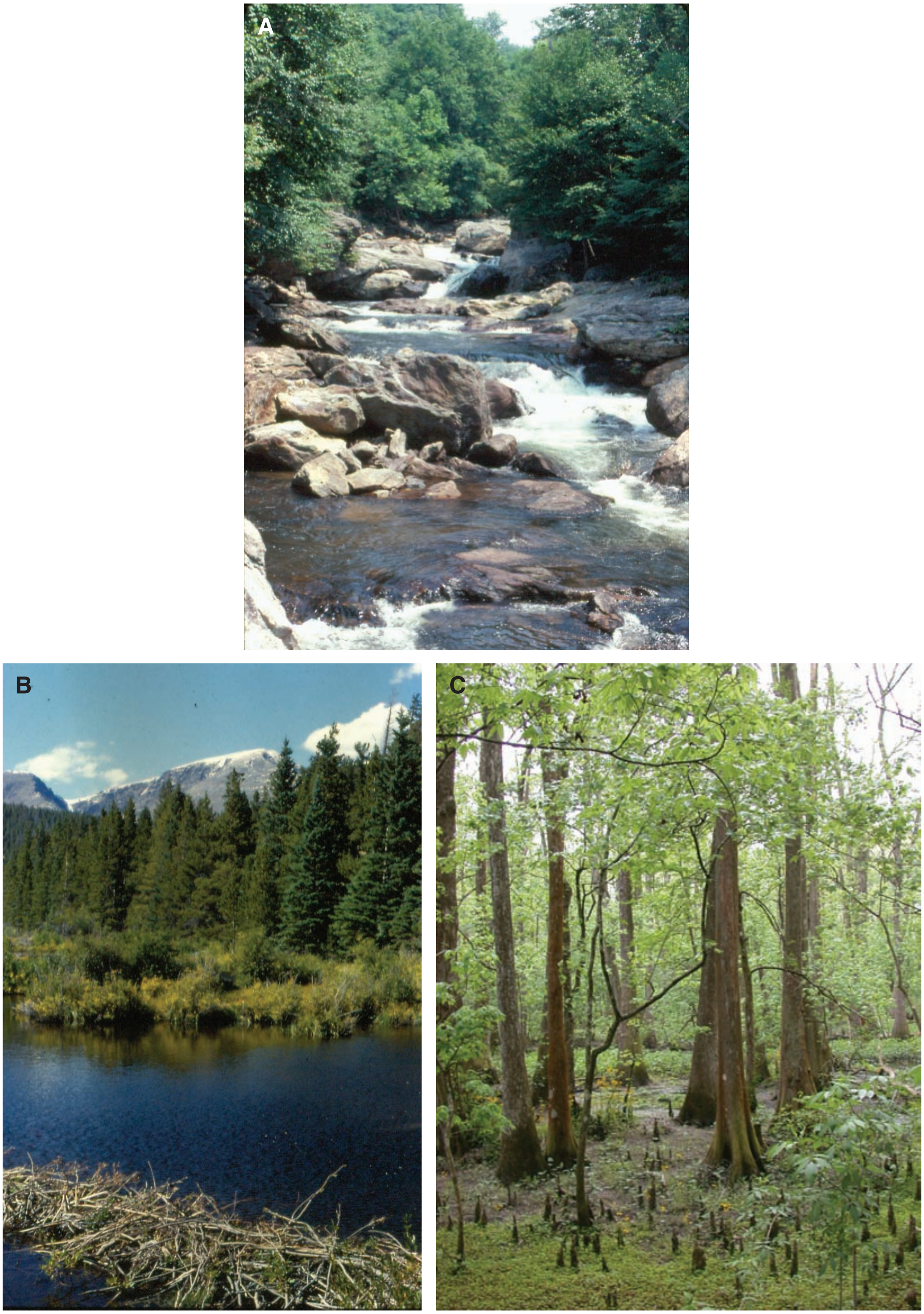


FIG. 2.6 Examples of aquatic biomes. **A:** Stream (western United States), **B:** beaver pond (western United States), **C:** swamp (southern United States), **D:** coastal saltmarsh (southeastern United States), **E:** lake (Hungary). Coastal saltmarsh photo *(D)* courtesy of S. D. Senter.

FIG. 2.6 (*Continued*)

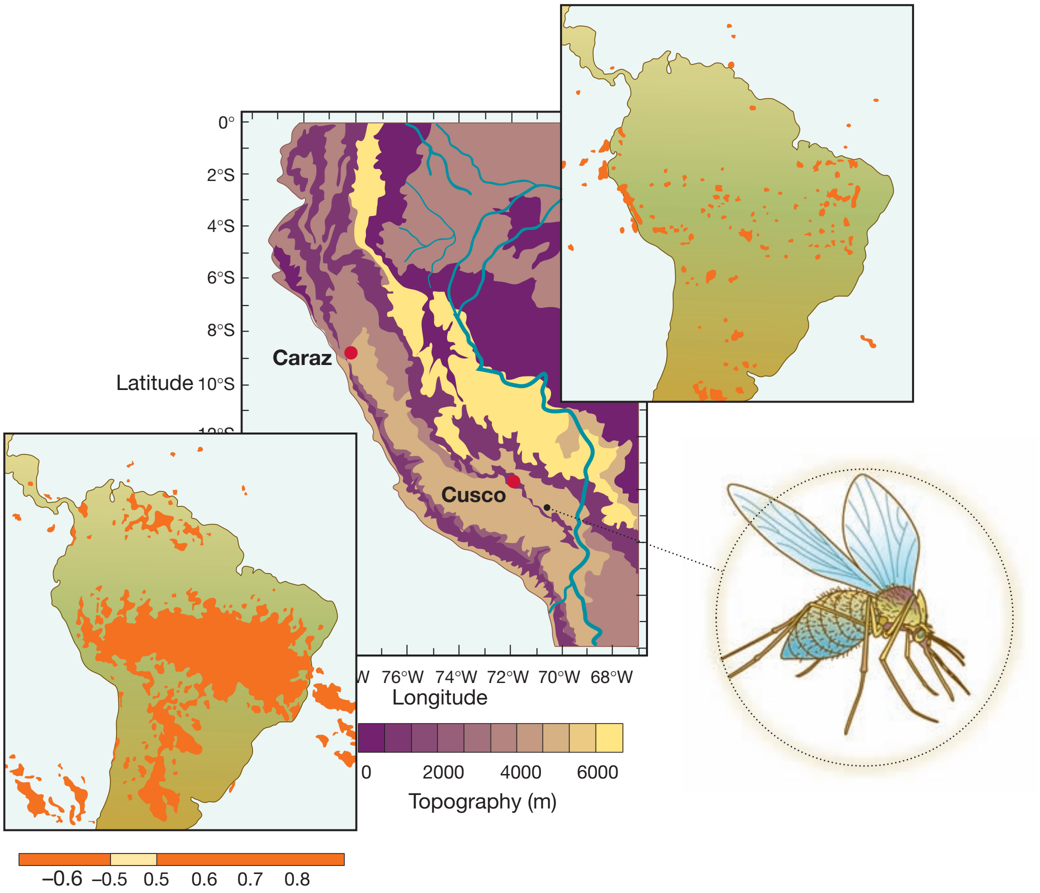


FIG. 2.7 Topography of Peru (*center*), comparison of TRMM (tropical rainfall measuring mission) TMI (tropical rainfall measuring mission microwave imager) rainfall at Cuzco (*lower left*) and Caraz (*upper right*) relative to their surroundings, and the sand fly, *Lutzomyia verrucarum*, vector of bartonellosis that shows increased spread associated with higher rainfall during El Niño events. Strong association of precipitation at Cuzco with monsoon system makes local sand fly abundance sensitive to El Niño events, whereas precipitation at Caraz, within the equatorial convergence zone, leads to more consistent abundance of sand flies. From Zhou *et al*. (2002) with permission from the American Geophysical Union. Please see extended permission list pg 569.

sparse vegetation cover usually show the widest diurnal and seasonal variation in physical conditions. Areas with high proportions of impervious surfaces (such as roads, roofs, parking lots) greatly alter conditions of both terrestrial and aquatic systems by increasing albedo and precipitation runoff (Elvidge *et al*. 2004).

Physiological tolerances of organisms, including insects, generally reflect the physical conditions of the biomes in which they occur. Insects associated with the tundra biome tolerate a lower range of temperatures than do insects associated with tropical biomes. The upper threshold temperature for survival of a tundra species might be the lower threshold temperature for survival of a tropical species. Similarly, insects characterizing mesic or aquatic biomes generally should have less tolerance for desiccation than do insects characterizing xeric biomes.

However, species characterizing temporary streams or ponds may have adapted mechanisms for withstanding desiccation during dry periods (Batzer and Wissinger 1996). Some species show greater capacity than others do to adapt to changing environmental conditions, especially rapid changes resulting from anthropogenic activity. Such species may be predisposed to adapt to rapid changes because of evolution in frequently disturbed ecosystems.

C. Disturbances

Within biomes, characteristic abiotic and biotic factors interact to influence the pattern of disturbances, relatively discrete events that alter ecosystem conditions, and create a finer-scale landscape mosaic of patches with different disturbance and recovery histories (Harding *et al*. 1998, Schowalter *et al*. 2003, Willig and Walker 1999). Disturbances, such as fire, storms, drought, flooding, anthropogenic conversion (Fig. 2.8), alter vertical and horizontal gradients in temperature, moisture, and air or water chemistry (T. Lewis 1998, P. White and Pickett 1985), significantly altering the abiotic and biotic conditions to which organisms are exposed (Agee 1993, Schowalter 1985, Schowalter and Lowman 1999).

Disturbances can be characterized by several criteria that determine their effect on various organisms (see Walker and Willig 1999, P. White and Pickett 1985). Disturbance type, such as fire, drought, flood, or storm, determines which ecosystem components will be most affected. Above-ground versus below-ground species or terrestrial versus aquatic species are affected differently by fire versus flood. Intensity is the physical force of the event, whereas severity represents the effect on the ecosystem. A fire or storm of given intensity, based on temperature or wind speed, will affect organisms differently in a grassland versus a forest. Scale is the area affected by the disturbance and determines the rate at which organisms recolonize the interior portions of the disturbed area. Frequency is the mean number of events per time period; reliability is measured as the inverse of variability in the time between successive events (recurrence interval).

Insects show a variety of adaptations to particular disturbance type. Some species respond positively, and others respond negatively to particular disturbances, based on adaptive characteristics (E. Evans 1988, Paquin and Coderre 1997, Schowalter *et al*. 1999, Wikars and Schimmel 2001). Responses differ between disturbance types. For example, Paquin and Coderre (1997) compared forest floor arthropod responses to forest clearing versus fire. Decomposers were less abundant, whereas predators were more abundant in cleared plots, relative to undisturbed plots. Arthropod abundance was reduced 95.5% following experimental fire, but some organisms survived as a result of occurrence in deeper soil levels or because of the patchy effect of fire. Abundances of some species differed between cleared and burned plots.

Following disturbance-induced change, populations and communities tend to become more similar to their starting point over time through a process known as ecological succession (see Chapter 10). Insect responses to anthropogenic dis-

FIG. 2.8 Natural disturbances include **A:** fire, especially in grasslands and savannas (north central United States), **B:** storms (north central United States), and **C:** floods (northwestern United States). Anthropogenic disturbances include the following: **D:** arid land conversion to agriculture use (center-pivot irrigation; western United States), **E:** forest harvest fragmentation (northwestern United States), and **F:** overgrazing and desertification (right of fence, compared to natural grassland on left; southwestern United States). These disturbances affect ecosystem components differentially. Adapted species survive, whereas nonadapted species may disappear. Overgrazing and desertification photo (*F*) courtesy of D. C. Lightfoot.

turbances reflect their adaptations to natural disturbances (e.g., forest harvest often elicits responses similar to other canopy opening disturbances); vegetation conversion to crop production elicits insect responses to changes in host density and apparency (see later in this chapter); and river impoundment elicits responses similar to landslides, which also alter drainage pattern. However, some anthropogenic disturbances are unique. Aquatic organisms historically had min-

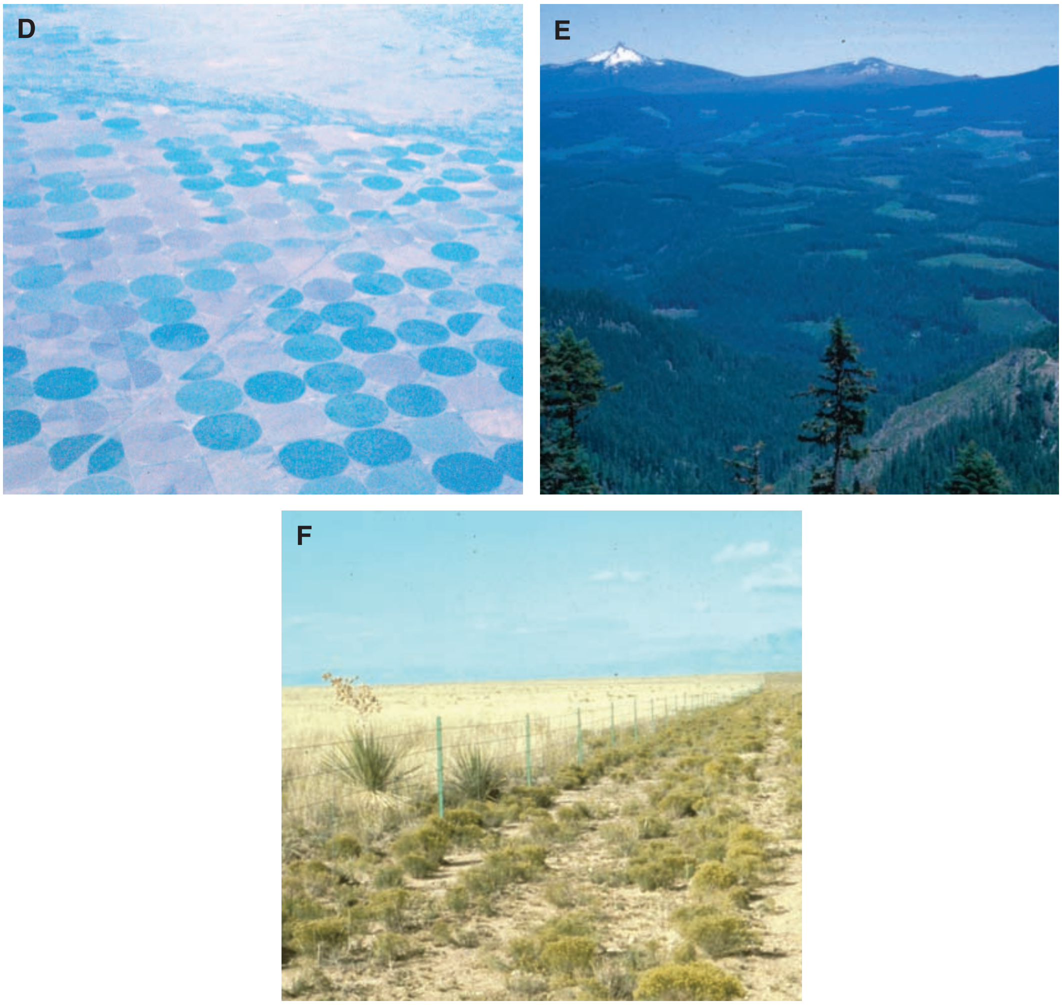


FIG. 2.8 (*Continued*)

imal exposure to the variety of synthetic toxins recently introduced into aquatic systems. Fires and other natural disturbances do not generate large numbers of stumps with exposed surfaces and in-ground root systems. Paving previously vegetated surfaces has created the most extreme changes in habitat conditions for organisms sensitive to high temperature and desiccation.

The effects of such changes may be difficult to predict, based on adaptations to natural disturbances, and may persist for long periods because local mechanisms are lacking for reversal of extreme alteration of vegetation, substrate, or water conditions. For example, Harding *et al*. (1998) reported that responses of aquatic invertebrate communities to restoration treatments reflected differences in community structure among stream segments with different histories of anthropogenic disturbances. Similarly, Schowalter *et al*. (2003) found that litter arthropod responses to variable density thinning of conifer forests for restoration purposes reflected different initial community structures, resulting from previous thinning as much as 30 years earlier.

Disturbances vary in intensity and severity. A low-intensity ground fire affects primarily surface-dwelling organisms, many of which may be adapted to this level of disturbance, whereas a high-intensity crown fire can destroy a large proportion of the community. Plant species capable of withstanding low-to-moderate wind speeds may topple at high wind speeds. Hurricane winds damage large areas of forest and can virtually eliminate many arthropods (Koptur *et al.* 2002, Willig and Camilo 1991).

Disturbances range in scale from local to global. Local disturbances affect the patchwork of communities that compose an ecosystem; global disturbances such as El Niño/La Niña events have far-reaching effects on climate fluctuation. Anthropogenic disturbances range from local conversion of ecosystems, such as altered streamflow pattern (e.g., sedimentation or stream scour resulting from coffer dam construction for logging), to global pollution and effects of fossil fuel combustion on climate. The degree of ecosystem fragmentation resulting from land-use changes is unprecedented in nature and seriously affects population distribution by reducing habitat area, isolating demes, and interfering with dispersal, potentially threatening species incapable of surviving in increasingly inhospitable landscapes (Samways *et al.* 1996, Shure and Phillips 1991, A. Suarez *et al.* 1998, Summerville and Crist 2001).

Frequency and reliability of recurrence, with respect to generation times of characteristic organisms, of a particular disturbance type probably are the most important factors driving directional selection for adaptation to disturbance (e.g., traits that confer tolerance [resistance] to fire or flooding). Effects of disturbances may be most pronounced in ecosystems, such as mesic forests and lakes, which have the greatest capacity to modify abiotic conditions and, therefore, have the lowest exposure and species tolerances to sudden or extreme departures from nominal conditions.

Individual insects have specific tolerance ranges to abiotic conditions that dictate their ability to survive local conditions but may be exposed during some periods to lethal extremes of temperature, water availability, or other factors. Variable ecosystem conditions usually select for wider tolerance ranges than do more stable conditions. Although abiotic conditions can affect insects directly (e.g., burning, drowning, particle blocking of spiracles), they also affect insects indirectly through changes in resource quality and availability and exposure to predation or parasitism (e.g., Alstad *et al.* 1982, K. Miller and Wagner 1984, Mopper *et al.* 2004, Shure and Wilson 1993). The degree of genetic heterogeneity affects the number of individuals that survive altered conditions. As habitat conditions change, intolerant individuals disappear, leaving a higher frequency of genes for tolerance of the new conditions in the surviving population. Adapted colonists also may arrive from other areas.

Some species are favored by altered conditions, whereas others may disappear. Sap-sucking insects become more abundant, but Lepidoptera, detritivores, and predators become less abundant, following canopy-opening disturbances in forests (Schowalter 1995, Schowalter and Ganio 2003). However, individual species within these groups may respond quite differently. Among Homoptera, some scale insects increase in numbers and others decline in numbers following canopy disturbance. Schowalter *et al.* (1999) found that species within each resource functional group responded differentially to manipulated change in moisture availability in a desert ecosystem (i.e., some species increased in abundance, whereas other species decreased or showed no change). Root bark beetles (e.g., *Hylastes nigrinus*) are attracted to chemicals, emanating from exposed stump surfaces, that advertise suitable conditions for brood development and become more abundant following forest thinning (Fig. 2.9) (Witcosky *et al.* 1986). Conversely, stem-feeding bark beetles (e.g., *Dendroctonus* spp.) are sensitive to tree spacing and become less abundant in thinned forests (Amman *et al.* 1988, Sartwell and Stevens 1975, Schowalter and Turchin 1993).

Reice (1985) experimentally disturbed benthic invertebrate communities in a low-order stream in the eastern United States by tumbling cobbles in patches of stream bottom 0, 1, or 2 times in a 6-week period. Most insect and other invertebrate taxa decreased in abundance with increasing disturbance. Two invertebrate taxa increased in abundance following a single disturbance, but no taxa increased in abundance with increasing disturbance. However, all populations rebounded quickly following disturbance, suggesting that these taxa were adapted to this disturbance.

Timing of disturbances, relative to developmental stage, also affects insect responses. However, Martin-R. *et al.* (1999) reported that experimental fires set during different developmental stages of spittlebug, *Aeneolamia albofasciata*, in buffelgrass, *Cenchrus ciliaris*, grassland in Sonora, Mexico eliminated spittlebugs for at least 4 years after burning, regardless of developmental stage at the time of burning. Because survival and reproduction of individual insects determine population size, distribution, and effects on community and ecosystem processes, the remainder of this chapter focuses on the physiological and behavioral characteristics that affect individual responses to variable abiotic conditions.

II. SURVIVING VARIABLE ABIOTIC CONDITIONS

Insects are particularly vulnerable to changes in temperature, water availability, and air or water chemistry because of their relatively large ratios of surface area to volume. However, many insects can live within suitable microsites that buffer exposure to environmental changes. Insects in aquatic environments or deep in soil or woody habitats may be relatively protected from large changes in air temperature and relative humidity (e.g., Curry 1994, Seastedt and Crossley 1981a). High moisture content of soil can mitigate heat penetration and protect soil fauna.

Most insects are subject to environmental variability that includes periods of potentially lethal or stressful abiotic conditions. Therefore, maintaining optimal body temperature, water content, and chemical processes is a challenge for survival in variable environments. Insects possess a remarkable variety of physiological and behavioral mechanisms for surviving in variable environments.

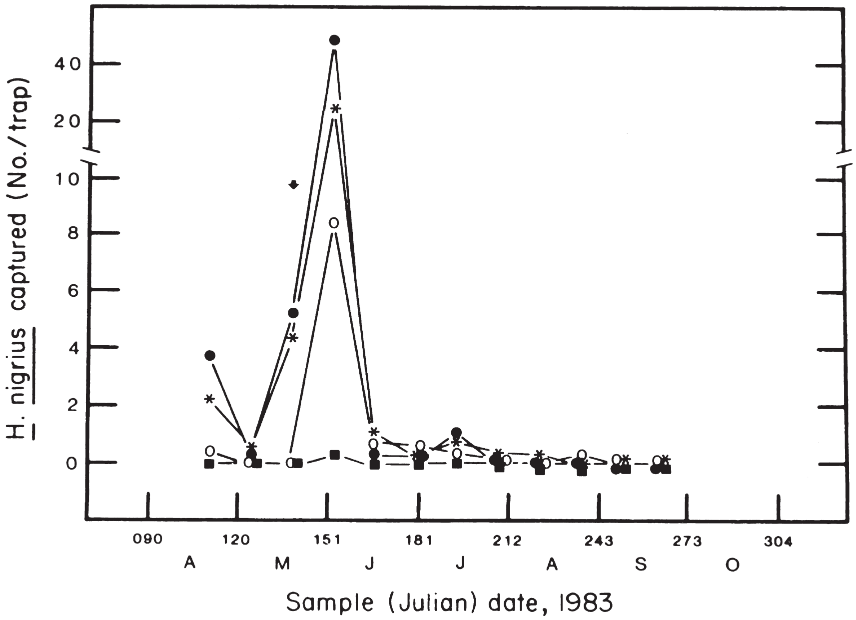


FIG. 2.9 Changes in abundance of a root bark beetle, *Hylastes nigrinus*, in undisturbed, 12-yr-old plantations (*black squares*) of Douglas fir and plantations thinned in September 1982 (*asterisks*), January 1983 (*black circles*), or May 1983 (*white circles*) in western Oregon. Arrow indicates time of thinning in May 1983. From Witcosky *et al.* (1986), courtesy of the Research Council of Canada.

Adaptive physiological responses can mitigate exposure to suboptimal conditions. For example, diapause is a general physiological mechanism for surviving seasonally adverse conditions, usually in a resistant stage, such as the pupa of holometabolous insects. Our understanding of the genetic and molecular basis for physiological processes has increased dramatically in the past 20 years. Diapause induction and termination are controlled by cues such as photoperiod and degree-day accumulation (daily degrees above a threshold temperature × number of days), which induce chemical signals from the brain (Denlinger 2002, Giebultowicz 2000, Giebultowicz and Denlinger 1986). In particular, photoreceptors that distinguish day from night trigger expression of genes that measure and accumulate information on day or night length, or both, and produce proteins that induce diapause (Hardie 2001). Denlinger (2002) and Giebultowicz (2000) reported that photoperiod affects patterns of expression, whereas temperature affects the amount, of several clock messenger ribonucleic acids (mRNAs; cryptochrome, *cry*; clock, *clk*; period, *per*; and timeless, *tim*), which also regulate circadian rhythms. The relative amounts of these mRNAs show distinct trends from long, warm days to shorter, cooler days, but their precise role in triggering the onset of diapause remains unknown (Denlinger 2002, Goto and Denlinger 2002). Various antibiotic proteins also are produced only during diapause, apparently to prevent infection during this vulnerable period, perhaps from tissue exposure to gut microorganisms while gut tissues are being reorganized (Dunn *et al*. 1994, Lee *et al*. 2002). Diapause termination often requires a minimum duration of freezing temperatures, or other factors, that maximize synchronization of development with seasonally suitable conditions (Ruberson *et al*. 1998). Beaver *et al*. (2002) reported that *Drosophila* males with mutated genes governing circadian rhythm produced fewer offspring than did wild flies, demonstrating the importance of the genes controlling periodicity. Nevertheless, exposed insects often are killed by sudden or unexpected changes in temperature, moisture, or chemical conditions of the habitat. Even diapausing insects suffer high mortality as a result of a combination of temperature, disease, predation, or other factors (Ruberson *et al*. 1998).

Behavior represents a more flexible means of responding to environmental variation, compared to physiology, because an animal can respond actively to sensory information to avoid or mitigate lethal conditions. Mobile insects have an advantage over sessile species in avoiding or mitigating exposure to extreme temperatures, water availability, or chemical conditions. Limited mobility often is sufficient within steep environmental gradients. Many small, flightless litter species need move vertically only a few millimeters within the soil profile to avoid lethal temperatures and desiccation at the surface following fire or canopy opening (Seastedt and Crossley 1981a). Some species choose protected habitats prior to entering diapause to reduce their vulnerability to potential disturbances. K. Miller and Wagner (1984) reported that pandora moth, *Coloradia pandora*, pupae in a ponderosa pine, *Pinus ponderosa*, forest were significantly more abundant on the forest floor in areas with open canopy and sparse litter than in areas with closed canopy and deeper litter. Although other factors also differ between these microhabitats, avoidance of accumulated litter may represent an adaptation to survive frequent ground fires in this ecosystem. In addition, mobile insects may be able to escape disturbed patches and often can detect and colonize suitable patches within variable environments (D. Johnson 2004).

Although small body size limits ability to regulate body temperature and water content, many insects are capable of at least limited homeostasis through physiological or behavioral mechanisms, or both. Some insects also must deal with variability in chemical or other abiotic conditions.

A. Thermoregulation

Insects, as well as other invertebrates, are generally heterothermic, meaning that their body temperatures are determined primarily by ambient temperature. Rates of metabolic activity (hence, energy and carbon flux) generally increase with temperature. Developmental rate and processes also are temperature dependent. However, at least some species regulate body temperature to some degree through physiological or behavioral responses to extreme temperatures.

Insect species show characteristic ranges in temperatures suitable for activity. Aquatic ecosystems have relatively consistent temperature, but insects in terrestrial ecosystems often experience considerable temperature fluctuation, even on a daily basis. As a group, insects can survive at temperatures from well below freezing to 40–50°C (Whitford 1992), depending on adapted tolerance ranges and acclimation (preconditioning). Some insects occurring at high elevations die at a maximum temperature of 20°C, whereas insects from warm environments often die at higher minimum temperatures. Chironomid larvae living in hot springs survive water temperatures of 49–51°C (R. Chapman 1982).

In general, developmental rate of heterotherms increases with temperature. Both terrestrial and aquatic insects respond to the accumulation of thermal units (the sum of degree-days above a threshold temperature) (Baskerville and Emin 1969, Ward 1992, Ward and Stanford 1982). Degree-day accumulation can be similar under different conditions (e.g., mild winter/cool summer and cold winter/hot summer) or quite different along elevational or latitudinal gradients. Anthropogenic conditions can significantly alter thermal conditions, especially in aquatic habitats. Discharge of heated water, artificial mixing of thermal strata, impoundment, diversion, regulation of water level and flow, and canopy opening in riparian zones, through harvest or grazing, severely modify the thermal environment for aquatic species and favor heat-tolerant individuals and species over heat-intolerant individuals and species (Ward and Stanford 1982).

A number of insects survive temperatures as low as –30°C, and some Arctic species survive below –50°C (N. Hadley 1994, Lundheim and Zachariassen 1993). Freeze-tolerant species can survive ice formation in extracellular fluids but not ice formation in intracellular fluids (N. Hadley 1994, Lundheim and Zachariassen 1993). Ice-nucleating lipids, lipoproteins, or both inhibit supercooling to ensure that ice forms in extracellular fluids at relatively high temperatures (i.e., above –10°C) (N. Hadley 1994). Extracellular freezing draws water osmotically from cells, thereby dehydrating cells and lowering the freezing point of intracellular fluids (N. Hadley 1994).

Other species have various mechanisms for lowering their freezing or supercooling points. Voiding the gut at the onset of cold conditions may prevent food particles from serving as nuclei for ice crystal formation. Similarly, nonfeeding stages may have lower supercooling points than do feeding stages (N. Hadley 1994, Kim and Kim 1997). Some insects prevent freezing to temperatures as low as –50°C by producing high concentrations (up to 25% of fresh weight) of alcohols and sugars, such as glycerol, glucose, and trehalose, as well as peptides and proteins in the hemolymph (N. Hadley 1994, Lundheim and Zachariassen 1993). In many cases, a multicomponent cryoprotectant system involving a number of compounds prevents accumulation of potentially toxic levels of any single component (N. Hadley 1994). Cold tolerance varies with life stage, temperature, and exposure time and can be enhanced by preconditioning to sublethal temperatures (Kim and Kim 1997). Rivers *et al.* (2000) reported that cold hardiness in a pupal parasitoid, *Nasonia vitripennis*, was enhanced by encasement within the flesh fly host, *Sarcophaga crassipalpi*, and by acquisition of host cryoprotectants, especially glycerol and alanine, during larval feeding.

Many insects also can reduce body temperature at high ambient temperatures, above 45°C (Casey 1988, Heinrich 1974, 1979, 1981, 1993). An Australian montane grasshopper, *Kosciuscola*, can change color from black at night to pale blue during the day (Key and Day 1954), thereby regulating heat absorption. Evaporative cooling, through secretion, regurgitation, ventilation, or other means, can lower body temperature 5–8°C below high ambient temperatures when the air is dry (N. Hadley 1994). Prange and Pinshow (1994) reported that both sexes of a sexually dimorphic desert grasshopper, *Poekiloceros bufonius*, depress their internal temperatures through evaporative cooling. However, males lost proportionately more water through evaporation, but retained more water from food, than did the much larger females, indicating that thermoregulation by smaller insects is more constrained by water availability.

Long-term exposure to high temperatures requires high body water content or access to water because death results from dessication at low humidity (R. Chapman 1982, N. Hadley 1994). N. Hadley (1994) described experiments demonstrating that males of a Sonoran Desert cicada, *Diceroprocta apache*, maintain evaporative cooling by ingesting xylem water from twigs on which they perch while singing. Although this species has high cuticular permeability, even at nonstressful temperatures, water loss ceases at death, indicating active cuticular pumping of body water. A 0.6-g cicada maintaining a temperature differential of 5°C must siphon at least 69 mg xylem fluid hour^{-1}. Laboratory experiments indicated that maintaining this temperature differential resulted in a 5% increase in metabolic rate over resting levels. These cicadas probably have additional energetic costs associated with rapid extraction and transport of ingested water to the cuticle.

Thermoregulation also can be accomplished behaviorally. Heinrich (1974, 1979, 1981, 1993) and Casey (1988) reviewed studies demonstrating that a variety of insects are capable of thermoregulation through activities that generate metabolic heat, such as fanning the wings and flexing the abdomen (Fig. 2.10). Flight can elevate body temperature 10–30°C above ambient (R. Chapman 1982, Heinrich 1993). A single bumble bee queen, *Bombus vosnesenskii*, can raise the temperature of the nest as much as 25°C above air temperatures as low as 2°C, even in the absence of insulating materials (Heinrich 1979).

Insects can sense and often move within temperature gradients to thermally optimal habitats. Light is an important cue that attracts insects to sources of heat or repels them to darker, cooler areas. Aquatic insects move both vertically and horizontally within temperature gradients to select sites of optimal temperatures (Ward 1992). Terrestrial insects frequently bask on exposed surfaces to absorb heat during early morning or cool periods and retreat to less exposed sites during warmer periods (Fig. 2.11). Some insects use or construct shelters to trap or avoid heat. Others burrow to depths at which diurnal temperature fluctuation is minimal (Polis *et al*. 1986). Seastedt and Crossley (1981a) reported significant redistribution of soil or litter arthropods from the upper 5 cm of the soil profile to deeper levels following canopy removal and consequent soil surface exposure and warming in a forested ecosystem. Tent caterpillars, *Malacosoma* spp., build silken tents that slow dissipation of metabolic heat and increase colony temperature above ambient (Fig. 2.12) (Fitzgerald 1995, Heinrich 1993). L. Moore *et al.* (1988) reported that overwintering egg masses and tents of the western tent caterpillar, *Malacosoma californicum*, occurred significantly more often on sides of trees, or isolated trees, exposed to the sun. Tents of overwintering larvae of the arctiid moth, *Lepesoma argentata*, occur almost exclusively in the exposed upper

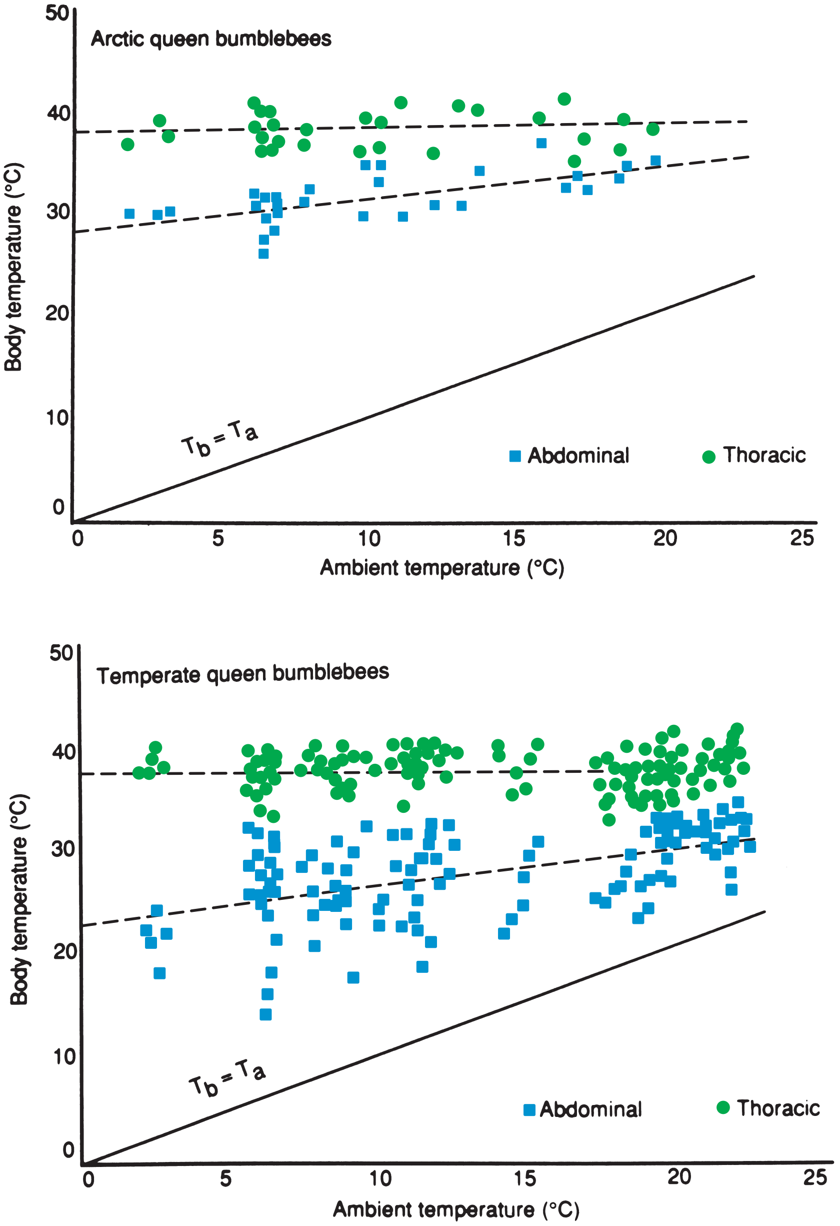


FIG. 2.10 Thermoregulation by insects. Thoracic and abdominal temperatures of high Arctic and temperate queen bumblebees foraging in the field as a function of air temperature; T_b = body temperature, T_a = ambient temperature. Arctic queens forage at significantly higher abdominal temperature than do temperate queens. From Heinrich (1993) with permission from Harvard University Press and Bernd Heinrich.

FIG. 2.11 Many insects, such as dragonflies, raise their body temperatures by basking. Heat absorption is enhanced by dark coloration and orientation. Photo courtesy of S. D. Senter.

canopy and significantly more often on the south-facing sides of host conifers in western Washington in the United States (D. Shaw 1998).

Some insects regulate body temperature by optimal positioning (Heinrich 1974, 1993). Web-building spiders adjust their posture to control their exposure to solar radiation (Robinson and Robinson 1974). Desert beetles, grasshoppers, and scorpions prevent overheating by stilting (i.e., extending their legs and elevating the body above the heated soil surface) and by orienting the body to minimize the surface area exposed to the sun (Heinrich 1993).

B. Water Balance

Maintenance of homeostatic water balance also is a challenge for organisms with high ratios of surface area to volume (Edney 1977, N. Hadley 1994). The arthropod exoskeleton is an important mechanism for control of water loss. Larger, more heavily sclerotized arthropods are less susceptible to desiccation than are smaller, more delicate species (Alstad *et al.* 1982, Kharboutli and Mack 1993).

Arthropods in xeric environments usually are larger, have a thicker cuticle, and secrete more waxes to inhibit water loss, compared to insects in mesic environments (Crawford 1986, Edney 1977, N. Hadley 1994, Kharboutli and Mack 1993). Cuticular lipids with higher melting points might be expected to be less permeable to water loss than are lipids with lower melting points. Gibbs (2002a)

FIG. 2.12 Tent caterpillars, *Malacosoma* spp., and other tent-constructing Lepidoptera reduce airflow and variation in temperatures within their tents.

evaluated cuticular permeability relative to water loss for several arthropod species and found that all species produced lipids with low melting points as well as high melting points, tending to increase water loss. Furthermore, lipids with high melting points did not reduce rates of water loss (Gibbs 2002a, Gibbs *et al.* 2003).

Some species in xeric environments conserve metabolic water (from oxidation of food) or acquire water from condensation on hairs or spines (R. Chapman 1982, N. Hadley 1994). Carbohydrate metabolism, to release bound water, increases several-fold in some insects subjected to desiccation stress (Marron *et al.* 2003). Others tolerate water loss of 17–89% of total body water content (Gibbs 2002b, N. Hadley 1994). Dehydration tolerance in *Drosophila* apparently reflects phylogeny rather than adaptation to desert environments (Gibbs and Matzkin 2001). Some insects regulate respiratory water loss by controlling spiracular activity under dry conditions (Fielden *et al.* 1994, N. Hadley 1994, Kharboutli and Mack 1993). Water conservation is under hormonal control in some species. An antidiuretic hormone is released in desert locusts, *Schistocerca gregaria*, and other species under conditions of water loss (Delphin 1965).

Gibbs *et al*. (2003) compared the three main water loss pathways among *Drosophila* species from xeric and mesic habitats. Excretory loss was <6% of the total and did not differ among species from different habitats. No consistent relationship was found between cuticular properties and water loss. Cuticular water loss rates did not appear to differ among flies from different habitats. Respiratory water loss differed significantly between xeric and mesic species. Xeric species of the same size had lower metabolic rates, were less active, and showed a cyclic pattern of CO_2 release, compared to mesic species, indicating adaptation to reduce respiratory loss.

Extreme dehydration may trigger the onset of *anhydrobiosis*, a physiological state characterized by an absence of free water and of measurable metabolism (N. Hadley 1994, Whitford 1992). Survival during anhydrobiosis requires stabilization of membranes and enzymes by compounds other than water (e.g., glycerol and trehalose), whose synthesis is stimulated by dehydration (N. Hadley 1994). Anhydrobiosis is common among plant seeds, fungi, and lower invertebrates, but among insects only some larval Diptera and adult Collembola have been shown to undergo anhydrobiosis (N. Hadley 1994). Hinton (1960a, b) reported that a chironomid fly, *Polypedilum vanderplancki*, found in temporary pools in central Africa, withstands repeated dehydration to 8% of body water content. At 3% body water content, this midge is capable of surviving temperatures from –270°C to 100°C, a range that contrasts dramatically with its tolerance range when hydrated.

Insects and other arthropods are most vulnerable to desiccation at times when a new exoskeleton is forming (i.e., during eclosion from eggs, during molts, and during diapause) (Crawford 1978, Willmer *et al*. 1996). Tisdale and Wagner (1990) found that percentage of sawfly, *Neodiprion fulviceps*, eggs hatched was significantly higher at relative humidities ≥50%. Yoder *et al*. (1996) found that slow water loss through the integument and respiration by diapausing fly pupae were balanced by passive water vapor absorption from the air at sufficiently high humidities. The ability of adult insects to regulate water loss may decline with age (Gibbs and Markow 2001).

Insects in diapause at subfreezing temperatures are subject to freeze-drying. Lundheim and Zachariassen (1993) reported that beetles that tolerate ice formation in extracellular fluids have lower rates of water loss than do insects that have supercooled body fluids, perhaps because the hemolymph in frozen beetles is in vapor pressure equilibrium with surrounding ice, whereas the hemolymph in supercooled insects has vapor pressure higher than the environment.

However, some insects must contend with excess water. Termites, ants, and other insects that live underground must survive periods of flooding. Subterranean termite species apparently survive extended periods of inundation by entering a quiescent state; relative abilities of species to withstand periods of flooding correspond to their utilization of above-ground or below-ground wood resources (Forschler and Henderson 1995).

Insects that ingest liquid food immediately excrete large amounts of water to concentrate dissolved nutrients. Elimination of excess water (and carbohydrates) in sap-feeding Homoptera is accomplished in the midgut by rapid diffusion

FIG. 2.13 Sap-feeding Homoptera, such as *Adelges cooleyi* on Douglas fir, egest excess water and carbohydrates as honeydew.

across a steep moisture gradient created by a filter loop (R. Chapman 1982). The resulting concentration of sugars in honeydew excreted by phloem-feeding Homoptera (Fig. 2.13) is an important resource for ants, hummingbirds, predaceous Hymenoptera, and sooty molds (Dixon 1985, E. Edwards 1982, N. Elliott *et al*. 1987, Huxley and Cutler 1991). The abundant water excreted by xylem-feeding spittlebugs is used to create the frothy mass that hides the insect. Excretion in some species, such as the blood-feeding *Rhodnius* (Heteroptera) is controlled by a diuretic hormone (Maddrell 1962).

Water balance also can be maintained behaviorally, to some extent, by retreating to cooler or moister areas to prevent desiccation. Burrowing provides access to more mesic subterranean environments (Polis *et al*. 1986). The small size of most insects makes them vulnerable to desiccation but also permits habitation within the relatively humid boundary layer around plant surfaces or at the soil surface.

Termites construct their colonies to optimize temperature and moisture conditions. Formosan subterranean termites, *Coptitermes formosanus*, prefer nest sites with high moisture availability (Fei and Henderson 1998). Metabolic heat generated in the core of the nest rises by convection into large upper cavities and diffuses to the sides of the nest where air is cooled and gaseous exchange occurs through the thin walls. Cooled air sinks into lower passages (Lüscher 1961). The interior chambers of termite colonies usually have high relative humidities.

C. Air and Water Chemistry

Air and water chemistry affect insect physiology. Oxygen supply is critical to survival but may be limited under certain conditions. Airborne or dissolved chemicals can affect respiration and development. Soil or water pH can affect exoskeleton function and other physiological processes. Changes in concentrations of various chemicals, especially those affected by industrial activities, affect many organisms, including insects.

Oxygen supply can limit activity and survival of aquatic species and some terrestrial species living in enclosed habitats. Less oxygen can remain dissolved in warm water than in cold water. Stagnant water can undergo oxygen depletion as a result of algal and bacterial respiration (Ward 1992). Some insect species living in oxygen-poor environments have more efficient oxygen delivery systems, such as increased tracheal supply, gills, or breathing tubes that extend to air supply (R. Chapman 1982, L. Chapman *et al.* 2004). For example, the hemolymph of some aquatic chironomid larvae and endoparasitic fly larvae is unique among insects in containing a hemoglobin that has a higher affinity for oxygen than does mammalian hemoglobin (R. Chapman 1982, Pinder and Morley 1995). Oxygen supply can be enhanced by ventilatory movement (i.e., movement of gills or other body parts to create currents that maintain oxygen supply and reduce the diffusion barrier) (Ward 1992). Other species must use siphon tubes (e.g., mosquito and syrphid fly larvae) or return to the surface (diving beetles) to obtain atmospheric oxygen (L. Chapman *et al.* 2004). Some wood-boring species must be able to tolerate low oxygen concentrations deep in decomposing wood, although O_2 limitation may occur only in relatively sound wood or water-soaked wood (Hicks and Harmon 2002).

Increased atmospheric CO_2 appears to have little direct effect on insects or other arthropods. However, relatively few insect species have been studied with respect to CO_2 enrichment. Increased atmospheric CO_2 can significantly affect the quality of plant material for some herbivore (Arnone *et al.* 1995, Bezemer and Jones 1998, Bezemer *et al.* 1998, Fajer *et al.* 1989, Kinney *et al.* 1997, Lincoln *et al.* 1993, Roth and Lindroth 1994) and decomposer (Grime *et al.* 1996, Hirschel *et al.* 1997) species, although plant response to CO_2 enrichment depends on a variety of environmental factors (e.g., Lawton 1995, Watt *et al.* 1995, see Chapter 3). In general, leaf chewers compensate for effects of elevated CO_2 by increasing consumption rates, whereas sap-suckers show reduced development times and increased population size (Bezemer and Jones 1998). At least some herbivorous species are likely to become more abundant and cause greater crop losses as a result of increased atmospheric CO_2 (Bezemer *et al.* 1998).

Airborne and dissolved materials can include volatile emissions or secretions from plant, animal, and industrial origin. Fluorides, sulfur compounds, nitrogen oxides, and ozone affect many insect species directly, although the physiological mechanisms of toxicity are not well-known (Alstad *et al.* 1982, Heliövaara 1986, Heliövaara and Väisänen 1986, 1993, Pinder and Morley 1995). Disruption of epicuticular or spiracular tissues by these reactive chemicals may be involved. Dust and ash kill many insects, apparently because they absorb and abrade the thin epicuticular wax-lipid film that is the principal barrier to water loss. Insects then die of desiccation (Alstad *et al.* 1982). V. C. Brown (1995) concluded that there is little evidence for direct effects of realistic concentrations of these major air pollutants on terrestrial herbivores, but there is considerable evidence that many herbivorous species respond to changes in the quality of plant resources or abundance of predators resulting from exposure to these pollutants. Kainulainen *et al.* (1994) found that exposure of Scots pine, *Pinus sylvestris*, seedlings to ozone significantly reduced amounts of starch and total amino acids at the highest ozone concentration (0.3 ppm), but it did not affect other sugars or other secondary compounds. Reproduction of grey pine aphids, *Schizolachnus pineti*, was not significantly affected by ozone exposure. However, pollutants may interfere with olfactory detection of hosts. Gate *et al.* (1995) exposed braconid parasitoids, *Asobara tabida*, to ozone, sulfur dioxide, and nitrogen dioxide in chambers with aggregations of its host, *Drosophila subobscura.* Ozone, but not sulfur dioxide or nitrogen dioxide, significantly reduced searching efficiency and the proportion of hosts that were parasitized. Parasitoids were able to avoid patches with no hosts but appeared to be less able to distinguish different host densities, indicating that air pollutants could reduce the effect of predation or parasitism.

Soil and water pH affect a variety of chemical reactions, including enzymatic activity. Changes in pH resulting from acidification (such as from volcanic or anthropogenic activity) affect osmotic exchange, gill and spiracular surfaces, and digestive processes. Changes in pH often are correlated with other chemical changes, such as increased N or S, and effects of pH change may be difficult to separate from other factors. Pinder and Morley (1995) reported that many chironomid species are relatively tolerant of alkaline water, but few are tolerant of $\text{pH} < 6.3$. Other aquatic species also may be unable to survive in low pH water (Batzer and Wissinger 1996). Acid deposition and loss of pH buffering capacity likely will affect survival and reproduction of aquatic and soil/litter arthropods (Curry 1994, Pinder and Morley 1995).

D. Other Abiotic Factors

Many aquatic insects are sensitive to water level and flow rate (Ward 1992). These factors can fluctuate dramatically, especially in seasonal habitats, such as desert playas, intermittent streams, wetlands, and perched pools in treeholes and bromeliads (phytotelmata). Water level affects both temperature and water quality, temperature because smaller volumes absorb or lose heat more quickly than do larger volumes, water quality because various solutes become more concentrated as water evaporates. Insects, and other aquatic arthropods, show life history adaptations to seasonal patterns of water availability or quality, often undergoing physiological diapause as water resources disappear (Batzer and Wissinger 1996, Ward 1992). Although most mosquitoes oviposit in surface water, floodwater mosquitoes, *Aedes* spp. and *Psorophora* spp., oviposit in soil at the high water line. Their eggs are resistant to desiccation and can remain dormant for several years. Egg hatch is stimulated by flooding, and the number of generations at a site depends on the frequency of flooding (Wiggins *et al.* 1980). Flow rate affects temperature and oxygenation, with cooler temperature and higher oxygen content at higher flow rates, but high flow rates can physically dislodge and remove

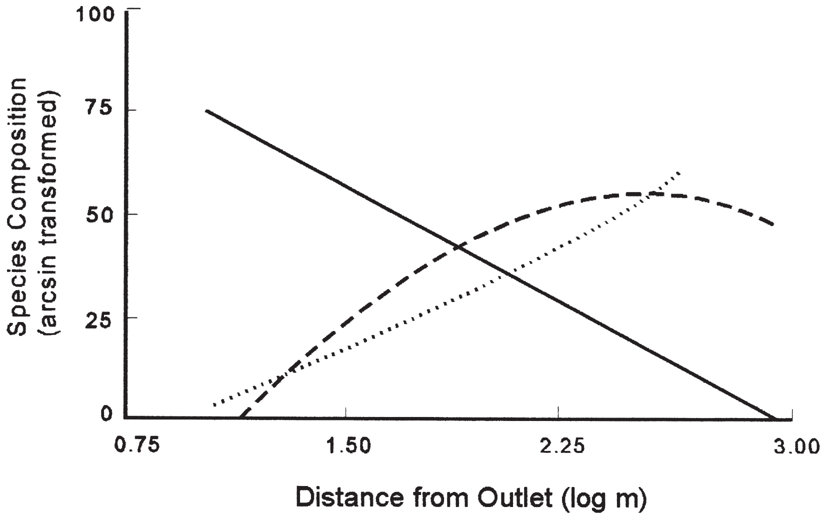


FIG. 2.14 Relationship between sibling species composition of black flies (*Simulium truncatum, solid line, S. verecundum* AA, *dashed line*, and *S. venustum* CC2, *dotted line*) and distance from lake outlets on the Avalon Peninsula, Newfoundland, in early June. Least squares regression equations were significant at $P < 0.01$; adjusted R^2 values were 92%, 85%, and 68% for the three species, respectively. From Adler and McCreadie (1997) with permission from the Entomological Society of America.

exposed insects. McCreadie and Colbo (1993) and Adler and McCreadie (1997) reported that sibling species of black flies, *Simulium*, select different stream microhabitats on the basis of their adaptations to water velocity (Fig. 2.14).

Light is an important factor affecting development, behavior, and distribution of many insects. Some aquatic insects are negatively phototactic during most of their lives, but they may move toward light under conditions of oxygen depletion (Ward 1992). Algal feeders are more likely to occur in illuminated portions of streams. Moonlight affects drift rates for species that disperse in stream currents and is a synchronizing agent for emergence of a number of aquatic species, especially nocturnal feeders, with different species emerging during different lunar phases (Ward 1992). A variety of insects are attracted to lights at night, an attribute that facilitates collection and measurement of diversity (see Chapter 9), and normal dispersal or foraging activities may be disrupted by artificial lights.

Insects are particularly sensitive to ultraviolet radiation. Kelly *et al.* (2003) demonstrated, using experimental filters, that aquatic insects in the Little Qualicum River on Vancouver Island showed differential sensitivities to ultraviolet A (UVA) and UVB exposure. Caddisflies (Trichoptera), especially *Dicosmoecus* spp. (Limnephillidae), were most sensitive to UV exposure. Final abundances under photosynthetically active radiation (PAR) alone were 15 times higher than under PAR + UVA and 40 times higher than under PAR + UVA + UVB. Stoneflies (Plecoptera) were 51% more abundant under PAR than under UV exposure. In contrast, chironomids (Diptera) were more abundant in the UV treatments.

III. FACTORS AFFECTING DISPERSAL BEHAVIOR

Insects have a considerable capacity to escape adverse conditions and to find optimal conditions within temperature, moisture, and chemical gradients across landscapes or watersheds. Dispersal is the movement of individuals away from their source. This is an important adaptive behavior that minimizes the risk that the entire population will be destroyed by disturbance or resource depletion, maximizes the chance that some individuals will find and exploit new resources, and maximizes genetic heterogeneity (D. Johnson 2004, Schowalter 1985, Wellington 1980; see Chapter 5).

Nevertheless, dispersal entails considerable risk and requires considerable energy expenditure (Rankin and Burchsted 1992). Torres (1988) documented cases of exotic insects being introduced into Puerto Rico by hurricane winds, including a swarm of desert locusts blown across the Atlantic Ocean from Africa. Many insects (and other organisms) fail to find or reach suitable habitats.

Flight capacity contributes enormously to insect ability to disperse. Adult aquatic insects can disperse from an intermittent pond or stream before the water disappears and search for other bodies of water. Dispersal may be particularly important for distributing populations and minimizing risk in ecosystems characterized by frequent disturbances. A number of factors affect the probability of successful dispersal (i.e., arrival at suitable habitats), including life history strategy, crowding, nutritional status, habitat and resource conditions, and the mechanism of dispersal.

A. Life History Strategy

The degree of adaptation to disturbance affects the predisposition of individuals to disperse. Species characterizing relatively stable, infrequently disturbed habitats tend to disperse slowly (i.e., produce few offspring and move short distances; see Chapter 5). Infrequent disturbance and consistent resource availability provide little or no selection for greater dispersal ability. Many forest species (especially Lepidoptera and Coleoptera) are flightless, or at least poor fliers. By contrast, species (such as aphids) that characterize temporary, frequently disturbed habitats produce large numbers of individuals and a high proportion of dispersers. Such traits are important adaptations for species exploiting temporary, unstable conditions (Janzen 1977).

B. Crowding

Crowding affects insect tendency to disperse, and in some cases it may stimulate morphological or physiological transformations that facilitate dispersal. Survival and fecundity are often density dependent (i.e., inversely related to population density). Therefore, dispersing individuals may achieve higher fitnesses than do nondispersing individuals at high population densities (Price 1997). For example, some bark beetle species oviposit their full complement of eggs in one tree under low-density conditions, but only a portion of their eggs in one tree under high-density conditions, leaving that tree and depositing remaining eggs in other trees (T. Wagner *et al*. 1981). If all eggs were laid in the first tree under crowded conditions, the large number of offspring could deplete resources before completing development.

Crowding has been shown to stimulate feeding and developmental rates. Under crowded conditions, some insects spend more time eating and less time resting (R. Chapman 1982). Crowding may increase the incidence of cannibalism in many species (Fox 1975a, b), encouraging dispersal. In addition, crowding can induce morphological changes that promote dispersal. Uncrowded desert locusts tend to repel one another and feed quietly on clumps of vegetation, whereas crowded locusts are more active, attract one another, and march en masse, spending little time on vegetation (Matthews and Matthews 1978). Accompanying physiological changes in color, wing length, and ability to feed on a wider variety of plants facilitate migration and the chances of finding suitable resources.

C. Nutritional Status

Nutritional status affects the endurance of dispersing insects. Populations of many insects show considerable variation in fat storage and vigor as a result of variation in food quality and the quantity and maternal partitioning of nutrient resources to progeny (T. Wagner *et al*. 1981, Wellington 1980). Many species exhibit obligatory flight distances that are determined by the amount of energy and nutrient reserves; dispersing individuals respond to external stimuli only after depleting these reserves to a threshold level. Hence, less vigorous individuals tend to colonize more proximal habitats, whereas more vigorous individuals fly greater distances and colonize more remote habitats. Because crowding and nutritional status are negatively related, the per capita accumulation of adequate energy reserves and the number of dispersing individuals should peak at intermediate densities when resource quality and quantity are still sufficient to promote insect development and vigor.

D. Habitat and Resource Conditions

The likelihood that an insect will find a suitable patch depends strongly on patch size and proximity to insect population sources. The probability of survival declines with distance, as a result of depletion of metabolic resources and protracted exposure to various mortality factors (Pope *et al*. 1980). Hence, more insects reach closer resources or sites. Sartwell and Stevens (1975) and Schowalter *et al*. (1981b) reported that, under nonoutbreak conditions, probability of bark beetle, *Dendroctonus* spp., colonization of living pine trees declined with distance from currently attacked trees. Trees more than 6 m from currently colonized trees had negligible probability of colonization by sufficient numbers to successfully kill the tree. Under outbreak conditions, the effect of distance disappeared (Schowalter *et al*. 1981b). Similarly, He and Alfaro (1997) reported that, under nonoutbreak conditions, colonization of white spruce by the white pine weevil, *Pissodes strobi*, depended on host condition and distance from trees colonized the previous year, but during outbreaks most trees were sufficiently near occupied trees to be colonized.

Larger or more conspicuous habitats or resources are more likely to be perceived by dispersing insects or to be intercepted by a given direction of flight (see Chapter 7). For example, Courtney (1985, 1986) reported that the pierid butterfly, *Anthocharis cardamines*, preferentially oviposited on the most conspicuous (in terms of flower size) host species that were less suitable for larval development than were less conspicuous hosts. This behavior by the adults represented a tradeoff between the prohibitive search time required to find the most suitable hosts and the reduced larval survival on the most conspicuous hosts. Larger habitat patches also intersect a longer arc centered on a given starting point. Insects dispersing in any direction have a higher probability of contacting larger patches than they do smaller patches.

E. Mechanism of Dispersal

The probability that suitable resources can be found and colonized depends on the mode of dispersal. Three general mechanisms can be identified: random, phoretic, and directed.

Random dispersal direction and path is typical of most small insects with little capacity to detect or orient toward environmental cues. Such insects are at the mercy of physical barriers or wind or water currents, and their direction and path of movement are determined by obstacles and patterns of air or water movement. For example, first instar nymphs of a *Pemphigus* aphid that lives on the roots of sea aster growing in salt marshes climb the sea asters and are set adrift on the rising tide. Sea breezes enhance movement, and successful nymphs are deposited at low tide on new mud banks where they seek new hosts (Kennedy 1975). Aquatic insect larvae often are carried downstream during floods. Hatching gypsy moth, *Lymantria dispar*, and other tussock moth larvae (Lymantriidae), scale insect crawlers, and spiders (as well as other arthropods) disperse by launching themselves into the airstream. Lymantriid and scale insect adults have poor (if any) flight capacity. The wind-aided dispersal by larval Lepidoptera and spiders is facilitated by extrusion of silk strands, a practice known as "ballooning." Western spruce budworm, *Choristoneura occidentalis*, adults aggregate in mating swarms above the forest canopy and are carried by wind currents to new areas (Wellington 1980).

The distance traveled by wind- or water-dispersed insects depends on several factors, including flow rate and insect size or mass. Jung and Croft (2001) measured falling speeds, relative to morphology and activity, of several wind-dispersed mite species. Heavier mites fell more rapidly than did lighter mites, as expected. However, anesthetized mites fell more rapidly than did active mites, indicating mite ability to control buoyancy and landing to some extent.

The probability that at least some insects will arrive at suitable resources depends on the number of dispersing insects and the predictability of wind or water movement in the direction of new resources. Most individuals fail to colonize suitable sites, and many become part of the aerial or aquatic plankton that eventually “falls out” and becomes deposited in remote, unsuitable locations. For example, J. Edwards and Sugg (1990) documented fallout deposition of many aerially dispersed insect species on montane glaciers in western Washington.

Phoretic dispersal is a special case in which a flightless insect or other arthropod hitches a ride on another animal (Fig. 2.15). Phoresy is particularly common among wingless Hymenoptera and mites. For example, scelionid wasps ride on the backs of female grasshoppers, benefiting from both transport and the eventual opportunity to oviposit on the grasshopper’s eggs. Wingless Mallophaga attach themselves to hippoboscid flies that parasitize the same bird hosts. Many species of mites attach themselves to dispersing adult insects that feed on the same dung or wood resources (Krantz and Mellott 1972, Stephen *et al.* 1993). The success of phoresy (as with wind- or water-aided dispersal) depends on the predictability of host dispersal. However, in the case of phoresy, success is enhanced by the association of both the hitchhiker and its mobile (and perhaps cue-directed) host with the same resource.

FIG. 2.15 Phoretic mesostigmatid mites on coxae of scarab beetle. Photo courtesy of A. Tishechkin.

Directed dispersal provides the highest probability of successful colonization and is observed in larger, stronger fliers capable of orienting toward suitable resources (see Chapter 3). Many wood-boring insects, such as wood wasps (Siricidae) and beetles (especially Buprestidae), are attracted to sources of smoke, infrared radiation, or volatile tree chemicals emitted from burned or injured trees over distances of up to several kilometers (W. Evans 1966, Gara *et al*. 1984, R.G. Mitchell and Martin 1980, Raffa *et al*. 1993, Wickman 1964). Attraction to suitable hosts often is significantly enhanced by mixing with pheromones emitted by early colonists (see Chapters 3 and 4). Visual or acoustic cues also may aid orientation. For example, masking the silhouette of tree boles (with white paint) substantially reduced numbers of attracted southern pine beetle, *Dendroctonus frontalis* (Strom *et al*. 1999), *Ips* engraver beetles, and some bark beetle predators (Goyer *et al*. 2004).

Migration is an active mass movement of individuals that functions to displace entire populations. Migration always involves females, but not always males. Examples of migratory behavior in insects include locusts, monarch butterflies, *Danaus plexippus*, and ladybird beetles. Locust, *Schistocerca gregaria* and *Locusta migratoria*, migration depends, at least in part, on wind patterns. Locust swarms remain compact, not because of directed flight, but because randomly oriented locusts reaching the swarm edge reorient toward the body of the swarm. Swarms are displaced downwind into equatorial areas where converging air masses rise, leading to precipitation and vegetation growth favorable to the locusts (Matthews and Matthews 1978). In this way, migration displaces the swarm from an area of crowding and insufficient food to an area with more abundant food resources. Monarch butterfly and ladybird beetle migration occurs seasonally and displaces large numbers to and from overwintering sites, Mexico for monarch butterflies and sheltered sites for ladybird beetles.

IV. RESPONSES TO ANTHROPOGENIC CHANGES

Insect responses to environmental changes caused by anthropogenic activity remain largely unknown. A number of studies have documented insect responses to elevated temperature; to increased atmospheric or aqueous concentrations of CO_2 or various pollutants, including pesticides; and to habitat disturbance and fragmentation (e.g., Alstad *et al*. 1982, Arnone *et al*. 1994, Bezemer and Jones 1998, Heliövaara and Väisänen 1986, 1993, Kinney *et al*. 1997, Lincoln *et al*. 1993, Marks and Lincoln 1996). As described earlier, the indirect effects of these changes may be greater than the direct effects.

Changing land-use patterns and ecosystem fragmentation alter abiotic variables and have the most dramatic effects on survival or movement of various insects (e.g., J. Chen *et al*. 1995, Franklin *et al*. 1992, Roland 1993, Rubenstein 1992). Kimberling *et al*. (2001) reported that physical disturbance related to construction or waste disposal had relatively less effect on invertebrate communities than did conversion of shrub-steppe to agricultural use in eastern Washington in the United States. Invasive species often are favored by habitat disturbance and subsequently change patterns of community interaction. For example, invasive red imported fire ants, *Solenopsis invicta*, are most abundant in disturbed habitats (Stiles and Jones 1998). Where abundant, they displace native ants, and negatively affect many ground nesting birds, small mammals, and herpetofauna, through aggressive foraging behavior, high reproductive rates, and lack of predators (C. Allen *et al*. 2004). A. Suarez *et al*. (2001) found that habitat fragmentation also favored the invasive Argentine ant, *Linepithema humile*, at the expense of native ant species. Summerville and Crist (2001) found that rare species were disproportionately affected by habitat fragmentation.

However, humans are changing environmental conditions in many ways simultaneously, through fossil fuel combustion, industrial effluents, water impoundment and diversion, pesticide application, and land-use practices. Large areas have been planted to genetically modified crops or occupied by invasive exotic species. Global atmospheric concentrations of CO_2 and other greenhouse gases are clearly increasing, and global climate has shown a distinct warming trend (e.g., Beedlow *et al*. 2004, Keeling *et al*. 1995). Acidic precipitation has greatly reduced the pH of many aquatic ecosystems in northern temperate countries, with more dramatic effects. Nitrogen subsidies resulting from increased atmospheric NO_x may provide a short-term fertilization effect in N-limited ecosystems until pH-buffering capacity of the soil is depleted. Deforestation, desertification, and other changes in regional landscapes are fragmenting habitats and altering habitat suitability for organisms around the globe (J. Foley *et al*. 2005).

The interactions between environmental factors are poorly understood but often synergistic. For example, deforestation changes surface albedo and leads to regional warming and drying in tropical biomes and to cooling in temperate and boreal biomes (J. Foley *et al*. 2003, 2005). Furthermore, studies in the Amazon basin indicate that smoke from fires that accompany forest conversion to agricultural or urban land use reduce cloud cover (from 38% in clean air to 0% in heavy smoke), reduce droplet size, and increase the altitude at which water condenses, leading to more violent thunderstorms and hail, rather than warm rain (Ackerman *et al*. 2000, Andreae *et al*. 2004, Koren *et al*. 2004). Altered drainage patterns affect temperature and chemical conditions of aquatic ecosystems and opportunities for organisms to disperse upstream or downstream (Pringle *et al*. 2000).

Few studies have measured insect responses to multiple changes in ecosystem conditions. However, given insect sensitivity to environmental changes, as described earlier, any change will alter insect abundance and distribution and may increase the incidence of crop pests and vectors of human and animal diseases (Stapp *et al*. 2004, Summerville and Crist 2001, D. Willliams and Liebhold 2002, Zhou *et al*. 2002). Chapin *et al*. (1987) addressed plant responses to multiple stressors and concluded that multiple factors can have additive or synergistic effects. We should expect some insects to disappear as habitat conditions exceed their tolerance ranges or their host plants disappear. Others will become more abundant and facilitate host plant decline by exploiting stressed and poorly defended hosts (see Chapter 3). Clearly, studies are needed on insect responses to multiple natural and anthropogenic changes to improve prediction of effects of environmental changes.

V. SUMMARY

Insects are affected by abiotic conditions that reflect latitudinal gradients in temperature and moisture, as modified by circulation patterns and mountain ranges. At the global scale, latitudinal patterns of temperature and precipitation produce bands of tropical rainforests along the equatorial convergence zone (where warming air rises and condenses moisture), deserts centered at 30°N and S latitudes (where cooled, dried air descends), and moist boreal forests centered at 60°N and S latitudes (where converging air masses rise and condense moisture). Mountains affect the movement of air masses across continents, forcing air to rise and condense on the windward side and dried air to descend on the leeward side. The combination of mountain ranges and latitudinal gradients in climatic conditions creates a template of regional ecosystem types known as biomes, characterized by distinctive vegetation (e.g., tundra, desert, grassland, forest). Aquatic biomes are distinguished by size, depth, flow rate, and marine influence (e.g., ponds, lakes, streams, rivers, estuaries).

Environmental conditions are not static but vary seasonally and annually. In addition, environment conditions change over longer periods as a result of global processes and anthropogenic activities. Acute events (disturbances), such as storm or fire, can dramatically alter habitat conditions and resource availability for various organisms. Hence, insects must be able to avoid or adjust to changing conditions.

The inherent problems of maintaining body heat and water content and avoiding adverse chemical conditions by small, heterothermic organisms have led to an astounding variety of physiological and behavioral mechanisms by which insects adjust to and interact with environmental conditions. Research on genetic control of physiological processes is improving our understanding of the mechanisms of adaptation. Mechanisms for tolerating or mitigating effects of variation in abiotic factors determine the seasonal, latitudinal, and elevational distributions of insect species.

Many insects have a largely unappreciated physiological capacity to cope with the extreme temperatures and relative humidities found in the harshest ecosystems on the planet. However, even insects in more favorable environments must cope with variation in abiotic conditions through diapause, color change, evaporative cooling, supercooling, voiding of the gut, control of respiratory water loss, etc. Many species exhibit at least limited homeostatic ability (i.e., ability to regulate internal temperature and water content).

Behavior represents the active means by which animals respond to their environment. Insects are sensitive to a variety of environmental cues, and most insects are able to modify their behavior in response to environmental gradients or changes. Insects, especially those that can fly, move within gradients of temperature, moisture, chemicals, or other abiotic factors to escape adverse conditions. Many species are able to regulate body heat or water content by using rapid muscle contraction, elevating the body above hot surfaces, seeking shade, or burrowing. Social insects appear to be particularly flexible in the use of colony activity and nest construction to facilitate thermoregulation.

Many insects are capable of flying long distances, but dispersal entails considerable risk, and many individuals do not reach suitable habitats. The probability that an insect will discover a suitable patch is a function of the tendency to disperse (as affected by life history strategy and crowding), endurance (determined by nutritional condition), patch size, distance, and the mechanism of dispersal (whether random, phoretic, or oriented toward specific habitat cues).

Environmental changes resulting from anthropogenic activities are occurring at an unprecedented rate. The effects of these changes on insects are difficult to predict because few studies have addressed the effects of multiple interacting changes on insects.

3

Resource Acquisition

ALL ORGANISMS ARE EXAMPLES OF NEGATIVE ENTROPY, IN CONTRAST TO the tendency for energy to be dissipated, according to the Second Law of Thermodynamics. Organisms acquire energy to collect resources and synthesize the organic molecules that are the basis for life processes, growth, and reproduction. Hence, the acquisition and concentration of energy and matter are necessary goals of all organisms and largely determine individual fitness.

Insects, like other animals, are heterotrophic (i.e., they must acquire their energy and material resources from other organisms; see Chapter 11). As a group, insects exploit a wide range of resources, including plant, animal, and detrital material, but individual organisms must find and acquire more limited, appropriate resources to support growth, maintenance, and reproduction.

The organic resources used by insects vary widely in quality (nutritional value), acceptability (preference ranking, given choices and tradeoffs), and availability (density and ease of detection by insects), depending on environmental conditions. Physiological and behavioral mechanisms for evaluating and acquiring food resources, and their efficiencies under different developmental and environmental conditions, are the focus of this chapter.

I. RESOURCE QUALITY

Resource quality is the net energy and nutrient value of food resources after accounting for an individual's ability (and energetic or nutrient cost) to digest the resource. The energy and nutrient value of organic molecules is a product of the number, elemental composition, and bonding energy of constituent atoms.

However, organic resources are not equally digestible into useable components. Some resources provide little nutritional value for the expense of acquiring and digesting them, and others cannot be digested by common enzymes. Many organic molecules are essentially unavailable, or even toxic, to a majority of organisms. Vascular plant tissues are composed largely of lignin and cellulose, digestible only by certain microorganisms. Nitrogen is particularly limiting to animals that feed on wood or dead plant material. Some organic molecules are cleaved into toxic components by commonly occurring digestive enzymes. Therefore, acquiring suitable resources is a challenge for all animals.

A. Resource Requirements

Insects feed on a wide variety of plant, animal, and dead organic matter. Dietary requirements for all insects include carbohydrates; amino acids; cholesterol; B vitamins; and inorganic nutrients, such as P, K, Ca, Na, etc. (R. Chapman 2003, Rodriguez 1972, Sterner and Elser 2002). Insects lack the ability to produce their own cellulases to digest cellulose. Nutritional value of plant material often is limited further by deficiency in certain requirements, such as low content of N (Mattson 1980), Na (Seastedt and Crossley 1981b, Smedley and Eisner 1995), or linoleic acid (Fraenkel and Blewett 1946). Resources differ in ratios among essential nutrients, resulting in relative limitation of some nutrients and potentially toxic levels of others (Sterner and Elser 2002). High lignin content toughens foliage and other tissues and limits feeding by herbivores without reinforced mandibles. Toxins or feeding deterrents in food resources increase the cost, in terms of search time, energy, and nutrients, necessary to exploit nutritional value.

For particular arthropods, several factors influence food requirements. The most important of these are the size and maturity of the arthropod and the quality of food resources. Larger organisms require more food and consume more oxygen per unit time than do smaller organisms, although smaller organisms consume more food and oxygen per unit biomass (Reichle 1968). Insects require more food and often are able to digest a wider variety of resources as they mature. Holometabolous species must store sufficient resources during larval feeding to support pupal diapause and adult development and, for some species, to support dispersal and reproduction by nonfeeding adult stages.

Some species that exploit nutritionally poor resources require extended periods (several years to decades) of larval feeding in order to concentrate sufficient nutrients (especially N and P) to complete development. Arthropods that feed on nutrient-poor detrital resources usually have obligate associations with other organisms that provide, or increase access to, limiting nutrients. Microbes can be internal or external associates. For example, termites host mutualistic gut bacteria or protozoa that catabolize cellulose, fix nitrogen, and concentrate or synthesize other nutrients and vitamins needed by the insect. Termites and some other detritivores feed on feces (coprophagy) after sufficient incubation time for microbial digestion and enhancement of nutritive quality of egested material. If coprophagy is prevented, these organisms often compensate by increasing consumption of detritus (McBrayer 1975). Aphids also may rely on endosymbiotic bacteria to provide requisite amino acids, vitamins, or proteins necessary for normal development and reproduction (Baumann *et al.* 1995).

B. Variation in Food Quality

Food quality varies widely among resource types. Plant material has relatively low nutritional quality because N usually occurs at low concentrations and most plant material is composed of carbohydrates in the form of indigestible cellulose and lignin. Woody tissues are particularly low in labile resources readily available to insects or other animals. Plant detrital resources may be impoverished in important nutrients as a result of weathering, leaching, or plant resorption prior to shedding senescent tissues.

Individual plants differ in their nutritional quality for a number of reasons, including soil fertility. Ohmart *et al.* (1985) reported that *Eucalyptus blakelyi* subjected to different N fertilization levels significantly affected fecundity of *Paropsis atomaria,* a chrysomelid beetle. An increase in foliar N from 1.5% to 4.0% increased the number of eggs laid by 500% and the rate of egg production by 400%. Similarly, Blumberg *et al.* (1997) reported that arthropod abundances were higher in plots receiving inorganic N (granular ammonium nitrate, rye grass cover crop) than in plots receiving organic N (crimson clover, *Trifolium incarnatum*, cover crop). However, the effects of plant fertilization experiments have been inconsistent, perhaps reflecting differences among plant species in their allocation of N to nutritive versus nonnutritive compounds or differences in plant or insect responses to other factors (Kytö *et al.* 1996, G. Waring and Cobb 1992).

The nutritional value of plant resources frequently changes seasonally and ontogenically. Filip *et al.* (1995) reported that the foliage of many tropical trees has higher nitrogen and water content early in the wet season than late in the wet season. R. Lawrence *et al.* (1997) caged several cohorts of western spruce budworm, *Choristoneura occidentalis,* larvae on white spruce at different phenological stages of the host. Cohorts that began feeding 3–4 weeks before budbreak and completed larval development prior to the end of shoot elongation developed significantly faster and showed significantly greater survival rate and adult mass than did cohorts caged later (Fig. 3.1). These results indicate that the phenological window of opportunity for this insect was sharply defined by the period of shoot elongation, during which foliar nitrogen, phosphorus, potassium, copper, sugars, and water were higher than in mature needles.

Food resources often are defended in ways that limit their utilization by consumers. Physical defenses include spines, toughened exterior layers, and other barriers. Spines and hairs can inhibit attachment or penetration by small insects or interfere with ingestion by larger organisms. These structures often are associated with glands that augment the defense by delivering toxins. Some plants entrap phytophagous insects in adhesives (R. Gibson and Pickett 1983) and may obtain nutrients from insects trapped in this way (Simons 1981). Toughened exteriors include lignified epidermis of foliage and bark of woody plants and heavily armored exoskeletons of arthropods. Bark is a particularly effective barrier to

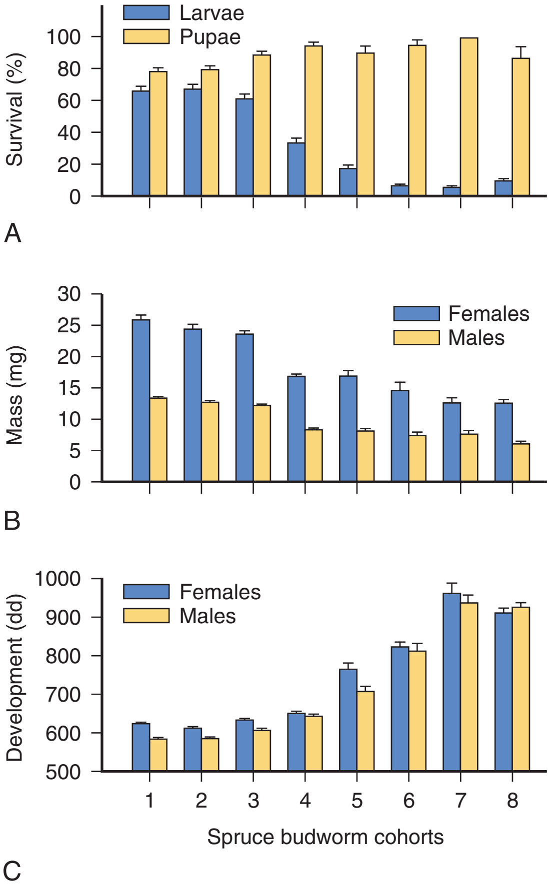


FIG. 3.1 Larval and pupal survival, adult dry mass, and development time from 2nd instar through adult for eight cohorts of spruce budworm caged on white spruce in 1985. The first six cohorts were started at weekly intervals beginning on Julian date 113 (April 23) for cohort 1. Cohort 7 started on Julian date 176 (June 25), and cohort 8 started on Julian date 204 (July 23). Each cohort remained on the tree through completion of larval development, 6–7 weeks. Budbreak occurred during Julian dates 118–136, and shoot elongation occurred during Julian dates 118–170. From R. Lawrence *et al.* (1997) by permission from the Entomological Society of Canada.

penetration by most organisms (Ausmus 1977), but lignin also reduces ability of many insects to use toughened foliage (e.g., Scriber and Slansky 1981). The viscous oleoresin (pitch) produced by conifers and some hardwoods can push insects out of plant tissues (Fig. 3.2).

Many plant and animal species are protected by interactions with other organisms, especially ants or endophytic fungi (see Chapter 8). A number of plant species provide food sources or habitable structures (domatia) suitable for colonies of ants or predaceous mites (e.g., Fischer *et al.* 2002, Huxley and Cutler 1991). Cecropia trees, *Cecropia* spp., in the tropics are one of the best-known plants protected by aggressive ants, *Azteca* spp., housed in its hollow stems (Rickson 1977). Central American acacias, *Acacia* spp, also are defended against

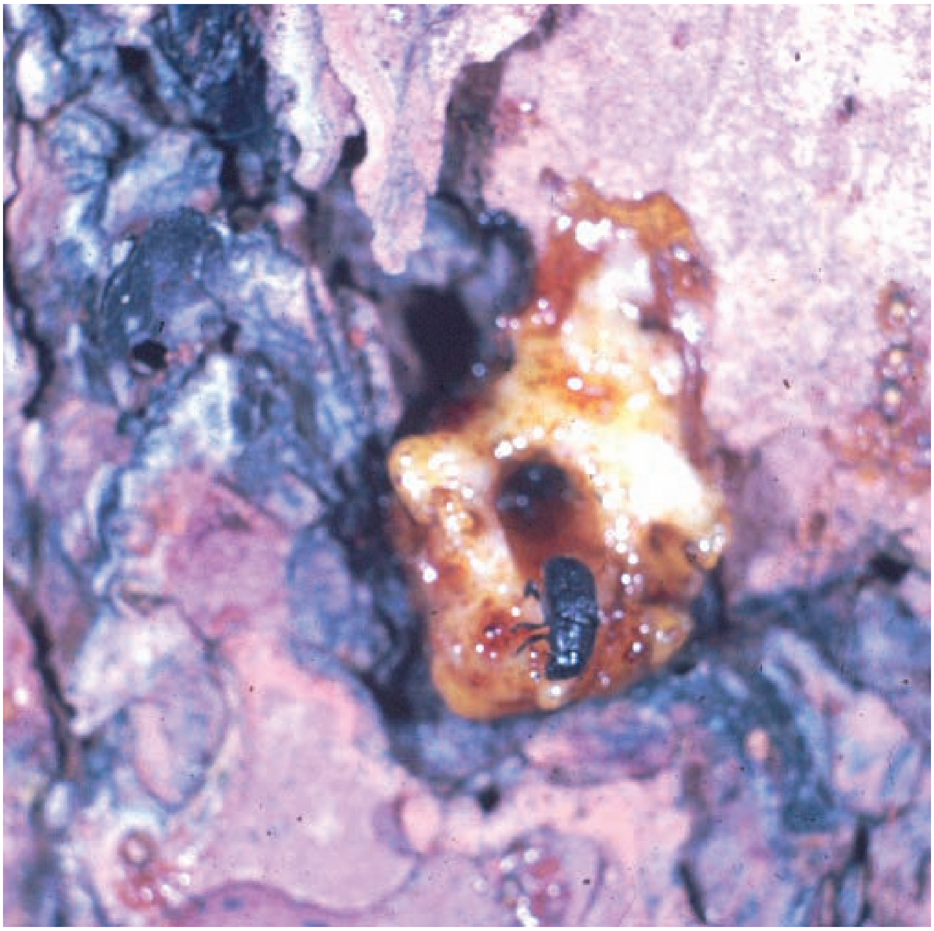


FIG. 3.2 The wound response of conifers constitutes a physical–chemical defense against invasion by insects and pathogens. The oleoresin, or pitch, flowing from severed resin ducts hinders penetration of the bark.

herbivores by colonies of aggressive ants, *Pseudomyrmex* spp., housed in swollen thorns (Janzen 1966). Many species of plants produce extrafloral nectaries or food bodies that attract ants for protection (Fischer *et al.* 2002). Some plants protect themselves from insect herbivores by emitting chemical signals that attract parasitic wasps (Kessler and Baldwin 2001, Turlings *et al.* 1993, 1995). G. Carroll (1988), Clay *et al.* (1993), and D. Wilson and Faeth (2001) have reported reduced herbivory by insects as a result of foliar infection by endophytic fungi.

Both plants and insects produce a remarkable range of compounds that have been the source of important pharmaceuticals or industrial compounds as well as effective defenses. These "secondary plant compounds" function as toxins or feeding deterrents, killing insects or slowing development rates, which may or may not increase exposure and effect of predators and parasites (Lill and Marquis 2001). Biochemical interactions between herbivores and their host plants and between predators and their prey have been one of the most stimulating areas of ecological and evolutionary research since the 1970s. Major points affecting ecological processes are summarized in the next section. Readers desiring additional information are referred to Bernays (1989), Bernays and Chapman (1994), K. Brown and Trigo (1995), Coley and Barone (1996), P. Edwards (1989), Harborne (1994), Hedin (1983), Kessler and Baldwin (2002), Rosenthal and Berenbaum (1991, 1992), and Rosenthal and Janzen (1979).

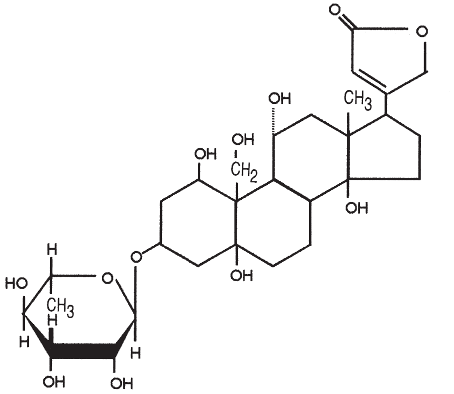
C. Plant Chemical Defenses

Plant chemical defenses generally are classified as nonnitrogenous, nitrogenous, and elemental. Ecologically, the distinction between nonnitrogenous and nitrogenous defenses reflects the availability of C versus N for allocation to defense at the expense of maintenance, growth, and reproduction. Each of these categories is represented by a wide variety of compounds, many differing only in the structure and composition of attached radicals. Elemental defenses are conferred by plant accumulation of toxic elements from the soil.

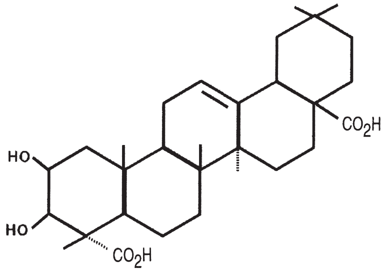
1. Nonnitrogenous Defenses

Nonnitrogenous defenses include phenolics, terpenoids, photooxidants, insect hormone or pheromone analogs, pyrethroids, and aflatoxins (Figs. 3.2–3.5). Phenolics, or flavenoids, are distributed widely among terrestrial plants and are likely among the oldest plant secondary (i.e., nonmetabolic) compounds. Although phenolics are perhaps best known as defenses against herbivores and plant pathogens, they also protect plants from damage by ultraviolet (UV) radiation, provide support for vascular plants (lignins), compose pigments that determine flower color for angiosperms, and play a role in plant nutrient acquisition by affecting soil chemistry. Phenolics include the hydrolyzeable tannins, derivatives of simple phenolic acids, and condensed tannins, polymers of higher molecular weight hydroxyflavenol units (Fig. 3.3). Polymerized tannins are highly resistant to decomposition, eventually composing the humic materials that largely determine soil properties. Tannins are distasteful, usually bitter and astringent, and act as feeding deterrents for many herbivores. When ingested, tannins chelate N-bearing molecules to form indigestible complexes (Feeny 1969). Insects incapable of catabolizing tannins or preventing chelation suffer gut damage and are unable to assimilate nitrogen from their food. Some flavenoids, such as rotenone, are directly toxic to insects and other animals.

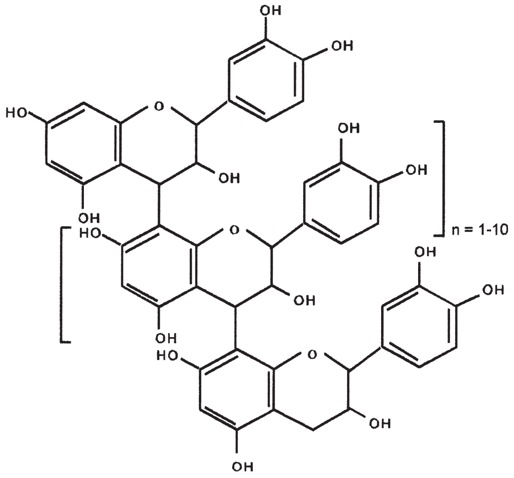
Rhoades (1977) reported that the foliage surface of creosotebushes, *Larrea tridentata* from the southwestern United States and *L. cuneifolia* from Argentina, is characterized by phenolic resins, primarily nordihydroquaiaretic acid. Young leaves contained about twice as much resin (26% d.w. for *L. tridentata,* 44% for *L. cuneifolia*) as did mature leaves (10% for *L. tridentata*, 15% for *L. cuneifolia*), but the amounts of nitrogen and water did not differ between leaf ages. Leaf-feeding insects that consume entire leaves all preferred mature foliage. Furthermore, extracting resins from foliage increased feeding on both young and mature leaves by a grasshopper generalist, *Cibolacris parviceps*, but reduced feeding on mature leaves by a geometrid specialist, *Semiothesia colorata*, in



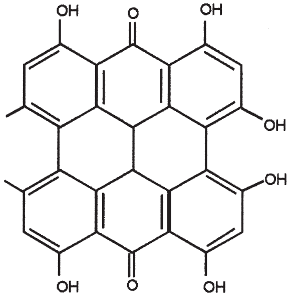
Terpenoid cardiac glycoside, ouabain, from *Acokanthera ouabaio*



Terpenoid saponin, medicagenic acid, from *Medicago sativa*

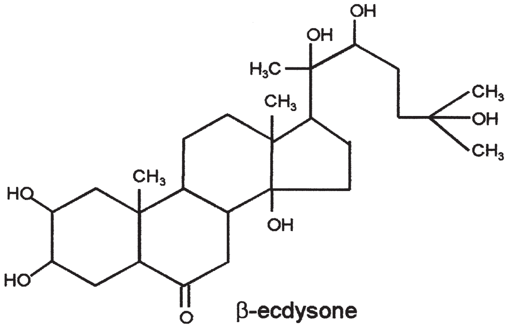


Flavonoid tannin, procyanidin, from *Quercus* spp.

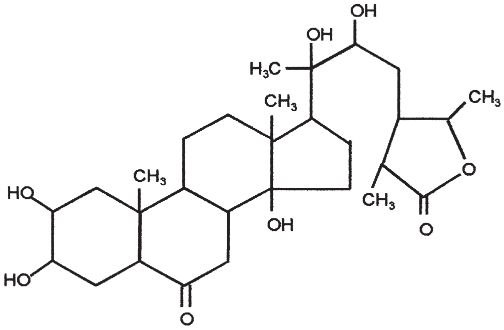


Quinone, hypericin, from *Hypericum perforatum*

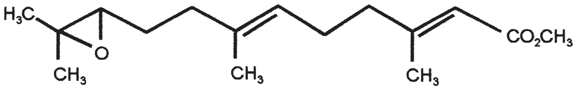
FIG. 3.3 Examples of nonnitrogenous defenses of plants. From Harborne (1994). Please see extended permission list pg 569.



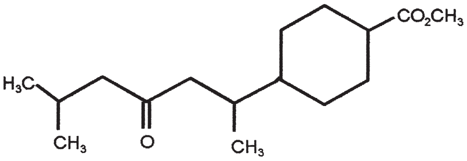
β-ecdysone



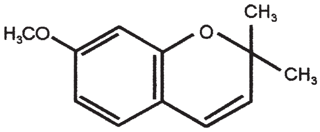
Cycasterone from *Cycas*



Juvenile hormone III

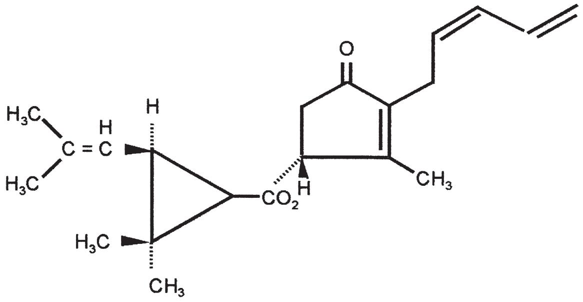


Juvabione from *Abies balsamea*

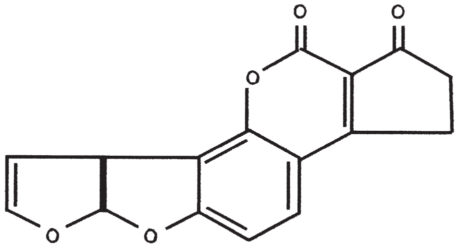


Precocene 1 from *Ageratum houstoniatum*

FIG. 3.4 Insect developmental hormones and examples of their analogues in plants. From Harborne (1994). Please see extended permission list pg 569.



Pyrethrin I, from *Chrysanthemum cinearifolium*



Aflatoxin B, from *Aspergillus flavus*

FIG. 3.5 Examples of pyrethroid and aflatoxin defenses. From Harborne (1994). Please see extended permission list pg 569.

laboratory experiments. These results suggested that low levels of resins in mature leaves may be a feeding stimulant for *S. colarata.*

Terpenoids also are widely represented among plant groups. These compounds are synthesized by linking isoprene subunits. The lower molecular weight monoterpenes and sesquiterpenes are highly volatile compounds that function as floral scents that attract pollinators and other plant scents that herbivores or their predators and parasites use to find hosts. Some insects modify plant terpenes for use as pheromones (see Chapter 4). Terpenoids with higher molecular weights include plant resins, cardiac glycosides, and saponins (Figs. 3.2 and 3.3). Terpenoids usually are distasteful or toxic to herbivores. In addition, they are primary resin components of pitch, produced by many plants to seal wounds. Pitch flow in response to injury by insect feeding can physically push the insect away, deter further feeding, kill the insect and associated microorganisms, or do all three (Nebeker *et al.* 1993).

Becerra (1994) reported that the tropical succulent shrub *Bursera schlechtendalii* stores terpenes under pressure in a network of canals in its leaves and stems. When these canals are broken during insect feeding, the terpenes are squirted up to 150 cm, bathing the herbivore and drenching the leaf surface. A specialized herbivore, the chrysomelid, *Blepharida* sp., partially avoids this defense by severing leaf veins before feeding but nevertheless suffers high mortality and may spend more time cutting veins than feeding, thereby suffering reduced growth.

Cardiac glycosides are terpenoids best known as the milkweed (Euphorbiaceae) compounds sequestered by monarch butterflies, *Danaus plexippus.* Ingestion of these compounds by vertebrates either induces vomiting or results in cardiac arrest. The butterflies thereby gain protection against predation by birds (L. Brower *et al.* 1968).

Photooxidants, such as the quinones (Fig. 3.3) and furanocoumarins, increase epidermal sensitivity to solar radiation. Assimilation of these compounds can result in severe sunburn, necrosis of the skin, and other epidermal damage on exposure to sunlight. Feeding on furanocoumarin-producing plants in daylight can cause 100% mortality to insects, whereas feeding in the dark causes only 60% mortality. Insect herbivores can circumvent this defense by becoming leaf rollers or nocturnal feeders (Harborne 1994) or by sequestering antioxidants (Blum 1992).

Insect development and reproduction are governed primarily by two hormones, molting hormone (ecdysone) and juvenile hormone (Fig. 3.4). The relative concentrations of these two hormones dictate the timing of ecdysis and the subsequent stage of development. A large number of phytoecdysones have been identified, primarily from ferns and gymnosperms. Some of the phytoecdysones are as much as 20 times more active than the ecdysones produced by insects and resist inactivation by insects (Harborne 1994). Schmelz *et al.* (2002) reported that spinach, *Spinacia oleracea*, produces 20-hydroxyecdysone in roots in response to root damage or root herbivory. Root feeding by the fly *Bradysia impatiens* increased production of 20-hydroxyecdysone by 4–6.6-fold. Fly larvae preferred a diet with a low concentration of 20-hydroxyecdysone and showed significantly reduced survival when reared on a diet with a high concentration of 20-hydroxyecdysone. Plants also produce some juvenile hormone analogues (primarily juvabione) and compounds that interfere with juvenile hormone activity (primarily precocene, Fig. 3.4). The antijuvenile hormones usually cause precocious development. Plant-derived hormone analogues are highly disruptive to insect development, usually preventing maturation or producing imperfect and sterile adults (Harborne 1994).

Some plants produce insect alarm pheromones that induce rapid departure of colonizing insects. For example, wild potato, *Solanum berthaultii*, produces (E)-β-farnesene, the major component of alarm pheromones for many aphid species. This compound is released from glandular hairs on the foliage at sufficient quantities to induce departure of settled colonies of aphids and avoidance by host-seeking aphids (R. Gibson and Pickett 1983).

Pyrethroids (Fig. 3.5) are an important group of plant toxins. Many synthetic pyrethroids are widely used as contact insecticides (i.e., absorbed through the exoskeleton) because of their rapid effect on insect pests.

Aflatoxins (Fig. 3.5) are toxic compounds produced by fungi. Many are highly toxic to vertebrates and, perhaps, to invertebrates (G. Carroll 1988, Harborne 1994). Higher plants may augment their own defenses through mutualistic associations with endophytic or mycorrhizal fungi that produce aflatoxins (G. Carroll 1988, Clay 1990, Clay *et al.* 1993).

2. Nitrogenous Defenses

Nitrogenous defenses include nonprotein amino acids, cyanogenic glucosides, glucosinolates, and alkaloids (Fig. 3.6). These compounds are highly toxic as a result of their interference with protein function or physiological processes.

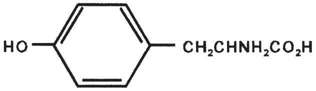
Nonprotein amino acids are analogues of essential amino acids (Fig. 3.6). Their substitution for essential amino acids in proteins results in improper configuration, loss of enzyme function, and inability to maintain physiological processes critical to survival. Some nonprotein amino acids are toxic for other reasons, such as interference with tyrosinase (an enzyme critical to hardening of the insect cuticle) by 3,4-dihydrophenylalanine (L-DOPA). More than 300 nonprotein amino acids are known, primarily from seeds of legumes (Harborne 1994).

Toxic or other defensive proteins are produced by many organisms. Proteinase inhibitors, produced by a variety of plants, interfere with insect digestive enzymes (Kessler and Baldwin 2002, Thaler *et al.* 2001). The endotoxins produced by the bacterium *Bacillus thuringiensis* (Bt) have been widely used for control of several Lepidoptera, Coleoptera, and mosquito pests. Because of their effectiveness, the genes coding for these toxins have been introduced into a number of crop plant species, including corn, sorghum, soybean, potato, and cotton, to control crop pests, raising concerns about potential effects of outcrossing between crop species and wild relatives or non-Bt refuges (Chilcutt and Tabashnik 2004) and potential effects on nontarget arthropods (Hansen Jesse and Obrycki 2000, Losey *et al.* 1999, Zangerl *et al.* 2001). However, subsequent studies have indicated minimal effect on nontarget species (O'Callaghan *et al.* 2005, Sears *et al.* 2001, Yu *et al.* 1997), and long-term regional suppression of major pests with Bt crops has greatly reduced the use of insecticides (Carrière *et al.* 2003).

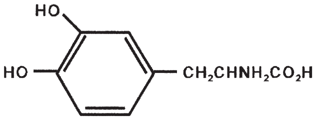
Cyanogenic glycosides are distributed widely among plant families (Fig. 3.6). These compounds are inert in plant cells. Plants also produce specific enzymes to control hydrolysis of the glycoside. When crushed plant cells enter the herbivore gut, the glycoside is hydrolyzed into glucose and a cyanohydrin that spontaneously decomposes into a ketone or aldehyde and hydrogen cyanide. Hydrogen cyanide is toxic to most organisms because of its inhibition of cytochromes in the electron transport system (Harborne 1994).

Glucosinolates, characteristic of the Brassicaceae, have been shown to deter feeding and reduce growth in a variety of herbivores (Renwick 2002, Strauss *et al.* 2004). Rotem *et al.* (2003) reported that young larvae of the cabbage white butterfly, *Pieris rapae,* a specialized herbivore, showed reduced growth with increasing glucosinolate concentration in *Brassica napus* hosts, but that older larvae were relatively tolerant of glucosinolates.

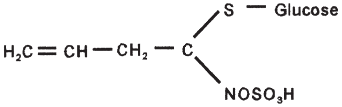
Alkaloids include more than 5000 known structures from about 20% of higher plant families (Harborne 1994). Molecules range in size from the relatively



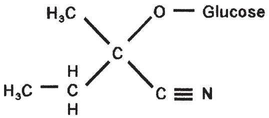
Protein amino acid, tyrosine



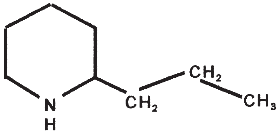
Non-protein amino acid, L-DOPA



Glucosinolate, sinigrin, from *Brassica campestris*



Cyanogenic glucoside, lotaustralin, from *Lotus corniculatus*



Alkaloid, coniine, from *Conium maculatum*

FIG. 3.6 Examples of nitrogenous defenses of plants. From Harborne (1994). Please see extended permission list pg 569.

simple coniine of poison hemlock (Fig. 3.6) to multicyclic compounds such as solanine. Familiar examples include atropine, caffeine, nicotine, belladonna, digitalis, and strychnine. They are highly toxic and teratogenic, even at relatively low concentrations, because of their interference with major physiological processes, especially cardiovascular and nervous system functions. D. Jackson *et al.* (2002) reported that larval weights and survival of tobacco budworm, *Helicoverpa virescens*, were negatively related to pyridine alkaloid concentrations among 18 tobacco, *Nicotiana tabacum*, cultivars. Survivorship after 8 weeks declined from 60% to 0% as total alkaloid concentration increased from 0% to 2% w.w. Shonle and Bergelson (2000) found that generalist herbivore feeding on *Datura stramonium* was negatively correlated with hyposcyamine concentration; however, feeding by specialist herbivores, flea beetles, *Epitrix* spp., was positively correlated with concentrations of scopolamine, indicating that this compound has become a phagostimulant for these adapted herbivores (see later in this chapter).

3. Elemental Defenses

Some plants accumulate and tolerate high concentrations of toxic elements, including Se, Mn, Cu, Ni, Zn, Cd, Cr, Pb, Co, Al, and As (Boyd 2004). In some cases, foliage concentrations of these metals can exceed 2% (Jhee *et al.* 1999). Although the function of such hyperaccumulation remains unclear, some plants benefit from protection against herbivores (Boyd 2004, Boyd and Moar 1999, Pollard and Baker 1997, Jhee *et al.* 2005).

Boyd and Martens (1994) found that larvae of the cabbage white butterfly fed *Thlaspi montanum* grown in high Ni soil showed 100% mortality after 12 days, compared to 21% mortality for larvae fed on plants grown in low Ni soil. Hanson *et al.* (2004) reported that Indian mustard, *Brassica juncea*, can accumulate Se up to 1000 mg kg^{-1} d.w., even from low-Se soils. Green peach aphids, *Myzus persicae*, avoided Se-containing leaves when offered a choice of foliage from plants grown in Se or non-Se soil. In nonchoice experiments, aphid population growth was reduced 15% at 1.5 mg Se kg^{-1} d.w. and few, if any, aphids survived at leaf concentrations >125 mg Se kg^{-1}. Jhee *et al.* (1999) found that young larvae of *Pieris napi* showed no preference for high- or low-Zn leaves of *Thlaspi caerulescens*, but later-instar larvae showed highly significant avoidance of high-Zn leaves. Jhee *et al.* (2005) concluded that Ni accumulation could protect *Streptanthus polygaloides* plants from chewing herbivores but not sap-sucking herbivores.

D. Arthropod Defenses

1. Antipredator Defenses

Arthropods also use various defenses against predators and parasites. Physical defenses include hardened exoskeleton, spines, claws, and mandibles. Chemical defenses are nearly as varied as plant defenses. Hence, predaceous species also must be capable of evaluating and exploiting defended prey resources. The compounds used by arthropods, including predaceous species, generally belong to the same categories of compounds described previously for plants.

Many insect herbivores sequester plant defenses for their own defense (Blum 1981, 1992; Boyd and Wall 2001). The relatively inert exoskeleton provides an ideal site for storage of toxic compounds. Toxins can be stored in scales on the wings of Lepidoptera (e.g., cardiac glycosides in the wings of monarch butterflies). Some insects make more than such passive use of their sequestered defenses. Sawfly (Diprionidae) larvae store the resinous defenses from host conifer foliage in diverticular pouches in the foregut and regurgitate the fluid to repel predators (Codella and Raffa 1993). Conner *et al.* (2000) reported that males of an arctiid moth, *Cosmosoma myrodora*, acquire pyrrolizidine alkaloids systematically from excrescent fluids of certain plants, such as *Eupatorium capillifolium* (but not from larval food plants) and discharge alkaloid-laden filaments from abdominal pouches on the female cuticle during courtship. This topical application significantly reduced predation of females by spiders, *Nephila clavipes,* compared to virgin females and females mated with alkaloid-free males. Additional alkaloid is transmitted to the female in seminal fluid and is partially invested in the eggs.

Accumulation of Ni from *Thlaspi montanum* by an adapted mirid plant bug, *Melanotrichus boydi*, protected it against some predators (Boyd and Wall 2001) but not against entomopathogens (Boyd 2002). L. Peterson *et al.* (2003) reported that grasshoppers and spiders, as well as other invertebrates, all had elevated Ni concentrations at sites where the Ni-accumulating plant, *Alyssum pintodasilvae*, was present but not at sites where this plant was absent, indicating spread of Ni through trophic interactions. Concentrations of Ni in invertebrate tissues approached levels that have toxic effects on birds and mammals, suggesting that using hyperaccumulating plant species for bioremediation may, instead, spread toxic metals through food chains at hazardous concentrations.

Many arthropods synthesize their own defensive compounds (Meinwald and Eisner 1995). A number of Orthoptera, Heteroptera, and Coleoptera exude noxious, irritating, or repellent fluids or froths when disturbed (Fig. 3.7). Blister beetles (Meloidae) synthesize the terpenoid, cantharidin, and ladybird beetles (Coccinellidae), synthesize the alkaloid, coccinelline (Meinwald and Eisner 1995). Both compounds are unique to insects. These compounds occur in the hemolymph and are exuded by reflex bleeding from leg joints. They deter both invertebrate and vertebrate predators. Cantharidin is used medicinally to remove warts. Whiptail scorpions spray acetic acid from their “tail,” and the millipede, *Harpaphe*, sprays cyanide (Meinwald and Eisner 1995). The bombardier beetle, *Brachynus*, sprays a hot (100°C) cloud of benzoquinone produced by mixing, at the time of discharge, a phenolic substrate (hydroquinone), peroxide, and an enzyme catalase (Harborne 1994).

Several arthropod groups produce venoms, primarily peptides, including phospholipases, histamines, proteases, and esterases, for defense as well as predation (Habermann 1972, Meinwald and Eisner 1995, Schmidt 1982). Both neurotoxic and hemolytic venoms are represented among insects. Phospholipases are particularly well-known because of their high toxicity and their strong antigen activity capable of inducing life-threatening allergy. Larvae of several families of Lepidoptera, especially the Saturniidae and Limacodidae (Fig. 3.8), deliver

FIG. 3.7 Defensive froth of an adult lubber grasshopper, *Romalea guttata.* This secretion includes repellent chemicals sequestered from host plants. From Blum (1997) with permission from the Entomological Society of America.

venoms passively through urticating spines, although defensive flailing behavior by many species increases the likelihood of striking an attacker. A number of Heteroptera, Diptera, Neuroptera, and Coleoptera produce orally derived venoms that facilitate prey capture, as well as defense (Schmidt 1982). Venoms are particularly well-known among the Hymenoptera and consist of a variety of enzymes, biogenic amines (such as histamine and dopamine), epinephrine, norepinephrine, and acetylcholine. Melittin, found in bee venom, disrupts erythrocyte membranes (Habermann 1972). This combination produces severe pain and affects cardiovascular, central nervous, and endocrine systems in vertebrates (Schmidt 1982). Some venoms include nonpeptide components. For example, venom of the red imported fire ant, *Solenopsis invicta*, contains piperidine alkaloids, with hemolytic, insecticidal, and antibiotic effects.

FIG. 3.8 Physical and chemical defensives of a limacodid (Lepidoptera) larva, *Isa textula.* The urticating spines can inflict severe pain on attackers.

2. *Antimicrobial Defenses*

Arthropods also defend themselves against internal parasites and pathogens. Major mechanisms include ingested or synthesized antibiotics (Blum 1992, Tallamy *et al.* 1998), gut modifications that prevent growth or penetration by pathogens, and cellular immunity against parasites and pathogens in the hemocoel (Tanada and Kaya 1993). Behavioral mechanisms also may be used for protection against pathogens.

Insects produce a variety of antibiotic and anticancer proteins capable of targeting foreign microorganisms (Boman *et al.* 1991, Boman and Hultmark 1987, Dunn *et al.* 1994, Hultmark *et al.* 1982, A. Moore *et al.* 1996, Morishima *et al.* 1995). The proteins are induced within as little as 30–60 minutes of injury or infection and can persist up to several days (Brey *et al.* 1993, Gross *et al.* 1996, Jarosz 1995). These proteins generally bind to bacterial or fungal membranes, increasing their permeability, and are effective against a wide variety of infectious organisms (Gross *et al.* 1996, Jarosz 1995, A. Moore *et al.* 1996). *Drosophila* spp. are known to produce more than 10 antimicrobial proteins (Cociancich *et al.* 1994).

Cecropin, originally isolated from the cecropia moth, *Hyalophora cecropia*, is produced in particularly large amounts immediately before, and during, pupation. Similarly, hemolin (from several moths) is produced in peak amounts during embryonic diapause in the gypsy moth, *Lymantria dispar* (K.Y. Lee *et al.* 2002). Peak concentration during pupation may function to protect the insect from exposure of internal organs to entomopathogens in the gut during diapause or metamorphosis (Dunn *et al.* 1994). In mosquitoes, cecropins may protect against some bloodborne pathogenic microfiliae (Chalk *et al.* 1995). The entomopathogenic nematode, *Heterorhabditis bacteriophora*—produces anticecropin to permit its pathogenic bacteria to kill the host, the greater wax moth, *Galleria mellonella* (Jarosz 1995).

Lepidoptera susceptible to the entomopathogenic bacterium, *Bacillus thuringiensis*, usually have high gut pH and large quantities of reducing substances and proteolytic enzymes, conditions that limit protein chelation by phenolics but that facilitate dissolution of the bacterial crystal protein and subsequent production of the delta-endotoxin. By contrast, resistant species have a lower gut pH and lower quantities of reducing substances and proteolytic enzymes (Tanada and Kaya 1993).

Cellular immunity is based on cell recognition of "self" and "nonself" and includes endocytosis and cellular encapsulation. Endocytosis is the process of infolding of the plasma membrane and enclosure of foreign substances within a phagocyte, without penetration of the plasma membrane. This process removes viruses, bacteria, fungi, protozoans, and other foreign particles from the hemolymph, although some of these pathogens then can infect the phagocytes. Cellular encapsulation occurs when the foreign particle is too large to be engulfed by phagocytes. Aggregation and adhesion by hemocytes form a dense covering around the particle. Surface recognition may be involved because parasitoid larvae normally protected (by viral associates) from encapsulation are encapsulated when wounded or when their surfaces are altered (Tanada and Kaya 1993). Hemocytes normally encapsulate hyphae of the fungus *Entomophthora egressa* but do not adhere to hyphal bodies that have surface proteins protecting them from attachment of hemocytes (Tanada and Kaya 1993).

Behavioral mechanisms include grooming and isolation of infected individuals. Grooming may remove ectoparasites or pathogens. Myles (2002) reported that eastern subterranean termites, *Reticulitermes flavipes*, rapidly aggregate around, immobilize, and entomb individuals infected by the pathogenic fungus *Metarhizium anisopliae*. Such behavior protects the colony from spread of the pathogen.

E. Factors Affecting Expression of Defenses

Some plant groups are characterized by particular defenses. For example, ferns and gymnosperms rely primarily on phenolics, terpenoids, and insect hormone analogues, whereas angiosperms more commonly produce alkaloids, phenolics, and many other types of compounds. However, most plants apparently produce compounds representing a variety of chemical classes (Harborne 1994, Newman 1990). Each plant species can be characterized by a unique "chemical fingerprint" conferred by these chemicals. Production of alkaloids and other physiologically active nitrogenous defenses depends on the availability of nitrogen (Harborne 1994). However, at least four species of spruce and seven species of pines are known to produce piperidine alkaloids (Stermitz *et al.* 1994), despite low N concentrations. Feeding by phytophagous insects can be reduced substantially by the presence of plant defensive compounds, but insects also identify potential hosts by their chemical fingerprint.

Defensive compounds may be energetically expensive to produce, and their production competes with production of other necessary compounds and tissues (e.g., Baldwin 1998, Chapin *et al.* 1987, Herms and Mattson 1992, Kessler and Baldwin 2002, Strauss and Murch 2004). Some, such as the complex phenolics and terpenoids, are highly resistant to degradation and cannot be catabolized to retrieve constituent energy or nutrients for other needs. Others, such as alkaloids and nonprotein amino acids, can be catabolized and the nitrogen, in particular, can be retrieved for other uses, but such catabolism involves metabolic costs that reduce net gain in energy or nutrient budgets. Few studies have addressed the fitness costs of defense. Baldwin (1998) evaluated seed production by plants treated or not treated with jasmonate, a phytohomone that induces plant defenses. Induction of defense did not significantly increase seed production of plants that came under herbivore attack but significantly reduced seed production of plants that were not attacked.

Given the energy requirements and competition among metabolic pathways for limiting nutrients, production of defensive compounds should be sensitive to risk of herbivory or predation and to environmental conditions (e.g., Chapin *et al.* 1987, Coley 1986, Coley *et al.* 1985, Hatcher *et al.* 2004, Herms and Mattson 1992, M. Hunter and Schultz 1995, Karban and Niiho 1995). Plants that support colonies of predaceous ants may reduce the need for, and cost of, chemical defenses. L. Dyer *et al.* (2001) reported that several amides produced by *Piper cenocladum* deter generalist herbivores, including leaf-cutting ants and orthopterans, whereas resident *Pheidole bicornis* ants deter specialist herbivores that oviposit on the plant. Plants hosting *P. bicornis* colonies produced lower concentrations of amides, indicating a tradeoff in costs between amides and support of ants. Nevertheless, redundant defenses are necessary to minimize losses to a diversity of herbivores.

Organisms are subjected to a variety of selective factors in the environment. Intense herbivory is only one factor that affects plant fitness and expression of defenses (Bostock *et al.* 2001). Plant genotype also is selected by climatic and soil conditions, various abiotic disturbances, etc. Factors that select intensively and consistently among generations are most likely to result in directional adaptation. The variety of biochemical defenses against herbivores testifies to the significance of herbivory in the past. Nevertheless, at least some biochemical defenses have multiple functions (e.g., phenolics as UV filters, pigments and structural components, as well as defense), implying that their selection was enhanced by meeting multiple plant needs. Similarly, insect survival is affected by climate, disturbances, condition of host(s), as well as a variety of predators. Short generation time confers a capacity to adapt quickly to strong selective factors, such as consistent and widespread exposure to particular plant defenses.

Plants balance the tradeoff between the expense of defense and the risk of severe herbivory (Coley 1986, Coley *et al.* 1985). Plants are capable of producing *constitutive defenses*, which are present in plant tissues at any given time and determine the "chemical fingerprint" of the plant, and *inducible defenses*, which are produced in response to injury (e.g., Haukioja 1990, Karban and Baldwin 1997, Klepzig *et al.* 1996, Nebeker *et al.* 1993, M. Stout and Bostock 1999, Strauss *et al.* 2004). Constitutive defenses consist primarily of relatively less specific, but generally effective, compounds, whereas inducible defenses are more specific compounds produced in response to particular types of injury (Hatcher *et al.* 2004). Induced defense is under the control of plant wound hormones, particularly jasmonic acid, salicylic acid, and ethylene (Creelman and Mullet 1997, Farmer and Ryan 1990, Karban and Baldwin 1997, Kessler and Baldwin 2002, Thaler 1999a, Thaler *et al.* 2001), that are triggered by injury or herbivore regurgitants (McCloud and Baldwin 1997). For example, pitch, consisting of relatively low–molecular weight terpenoids, is a generalized wound repair mechanism of many conifers that seals wounds, infuses the wound with constitutive terpenoids, and physically prevents penetration of the bark by insects (see Fig. 3.2). Successful penetration of this defense by bark beetles induces production of more complex phenolics that cause cell necrosis and lesion formation in the phloem and cambium tissues surrounding the wound and kill the beetles and associated microorganisms (Klepzig *et al.* 1996, Nebeker *et al.* 1993). Proteinase inhibitors are commonly induced by wounding and interfere with insect digestive enzymes (Kessler and Baldwin 2002, Thaler *et al.* 2001).

Studies indicate that plants often respond to injury with a combination of induced defenses that may be targeted against a particular herbivore or pathogen species but that also confer generalized defense against associated or subsequent herbivores or pathogens (Hatcher *et al.* 2004, Kessler and Baldwin 2002, M. Stout and Bostock 1999). Klepzig *et al.* (1996) reported that initial penetration of *Pinus resinosa* bark by bark beetles and associated pathogenic fungi was not affected by plant constitutive defenses but elicited elevated concentrations of phenolics and monoterpenes that significantly inhibited germination of fungal spores or subsequent hyphal development. Continued insect tunneling and fungal development elicited further host reactions that were usually sufficient to repel the invasion in healthy trees. Plant defenses can be induced through multiple pathways that encode for different targets, such as internal specialists versus more mobile generalists, and interaction ("crosstalk") among pathways may enhance or compromise defenses against associated consumers (Kessler and Baldwin 2002, Thaler 1999a, Thaler *et al.* 2001). Whereas emission of jasmonate from damaged plants can communicate injury and elicit production of induced defenses by neighboring, even unrelated, plants (see Chapter 8), herbivorous insects may not be able to detect, or learn to avoid, jasmonic acid (Daly *et al.* 2001).

Tissues vary in their concentration of defensive compounds, depending on risk of herbivory and value to the plant (Dirzo 1984, Feeny 1970, McKey 1979, Scriber and Slansky 1981, Strauss *et al.* 2004). Foliage tissues, which are the source of photosynthates and have a high risk of herbivory, usually have high concentrations of defensive compounds. Similarly, defensive compounds in shoots are concentrated in bark tissues, perhaps reducing risk to subcortical tissues, which have relatively low concentrations of defensive compounds (e.g., Schowalter *et al.* 1992).

Defensive strategies change as plants or tissues mature (Dirzo 1984, Forkner *et al.* 2004). A visible example is the reduced production of thorns on foliage and branches of acacia, locust, and other trees when the crown grows above the grazing height of vertebrate herbivores (Cooper and Owen-Smith 1986, P. White 1988). Seasonal growth patterns also affect plant defense. Concentrations of condensed tannins in oak, *Quercus* spp., leaves generally increase from low levels at bud break to high levels at leaf maturity (Feeny 1970, Forkner *et al.* 2004). This results in a concentration of herbivore activity during periods of leaf emergence (Coley and Aide 1991, Feeny 1970, M. Hunter and Schultz 1995, R. Jackson *et al.* 1999, Lowman 1985, 1992, McKey 1979). Lorio (1993) reported that production of resin ducts by loblolly pine, *Pinus taeda*, is restricted to latewood formed during summer. The rate of earlywood formation in the spring determines the likelihood that southern pine beetles, *Dendroctonus frontalis*, colonizing trees in spring will sever resin ducts and induce pitch flow. Hence, tree susceptibility to colonization by this insect increases with stem growth rate.

Concentrations of various defensive chemicals also change seasonally and annually as a result of environmental changes (Cronin *et al.* 2001, Mopper *et al.* 2004). Cronin *et al.* (2001) monitored preferences of a stem-galling fly, *Eurosta solidaginis*, among the same 20 clones of goldenrod, *Solidago altissima*, over a 12 year period and found that preference for, and performance on, the different clones was uncorrelated between years. These data indicated that genotype x environmental interaction affected the acceptability and suitability of clones for this herbivore.

Healthy plants growing under optimal environmental conditions should be capable of meeting the full array of metabolic needs and may provide greater nutritional value to insects capable of countering plant defenses. However, unhealthy plants or plants growing under adverse environmental conditions (such as water or nutrient limitation) may favor some metabolic pathways over others (e.g., Herms and Mattson 1992, Lorio 1993, Mattson and Haack 1987, Mopper *et al.* 2004, Tuomi *et al.* 1984, Wang *et al.* 2001, R. Waring and Pitman 1983). In particular, maintenance and replacement of photosynthetic (foliage), reproductive, and support (root) tissues represent higher metabolic priorities than does production of defensive compounds, under conditions that threaten survival. Therefore, stressed plants often sacrifice production of defenses so as to maximize allocation of limited resources to maintenance pathways and thereby become relatively more vulnerable to herbivores (Fig. 3.9).

However, N enrichment may permit plants to allocate more C to growth and reduce production of nonnitrogenous defenses, making plants more vulnerable to herbivores, as predicted by the *Carbon/nutrient balance hypothesis* (Holopainen *et al.* 1995). Plant fertilization experiments have produced apparently contradictory results (Kytö *et al.* 1996, G. Waring and Cobb 1992). In some cases, this inconsistency may reflect different insect feeding strategies (Kytö *et al.* 1996, Schowalter *et al.* 1999). Kytö *et al.* (1996) also found that positive responses to N fertilization at the individual insect level were often associated with negative responses at the population level, perhaps indicating indirect effects of fertilization on attraction of predators and parasites.

Spatial and temporal variability in plant defensive capability creates variation in food quality for herbivores (L. Brower *et al.* 1968). In turn, herbivore employment of plant defenses affects their vulnerability to predators (L. Brower

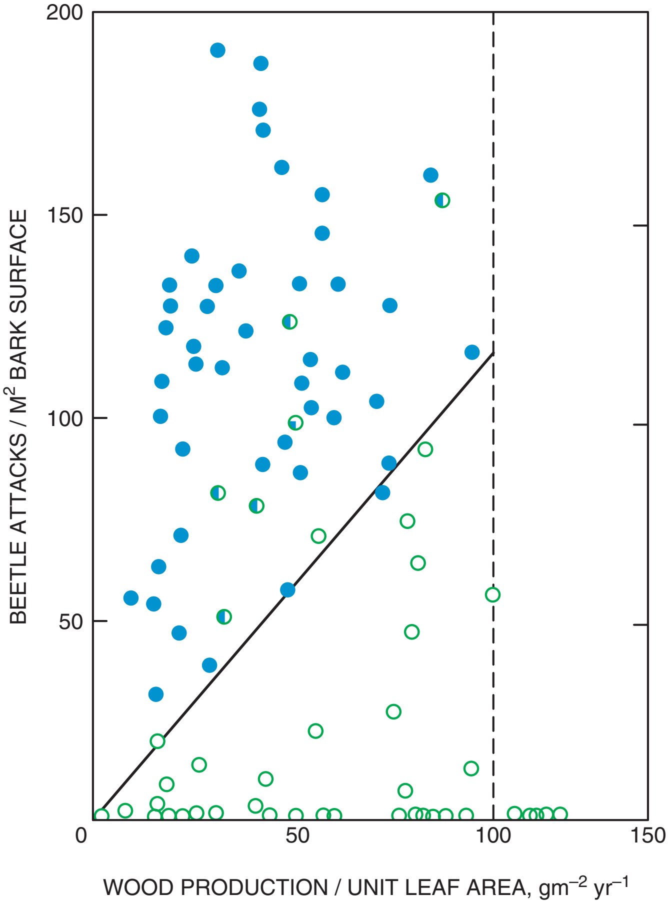


FIG. 3.9 The density of mountain pine beetle attacks necessary to kill lodgepole pine increases with increasing host vigor, measured as growth efficiency. The blackened portion of circles represents the degree of tree mortality. The solid line indicates the attack level predicted to kill trees of a specified growth efficiency (index of radial growth); the dotted line indicates the threshold above which beetle attacks are unlikely to cause mortality. From R. Waring and Pitman (1983) with permission from Blackwell Wissenschafts Verlag GmbH.

et al. 1968, Malcolm 1992, Stamp *et al.* 1997, Traugott and Stamp 1996). Herbivore feeding strategies represent a tradeoff between maximizing food quality and minimizing vulnerability to predators (e.g., Schultz 1983, see later in this chapter).

The frequent association of insect outbreaks with stressed plants, including plants stressed by atmospheric pollutants (e.g., V.C. Brown 1995, Heliövaara 1986, Heliövaara and Väisänen 1986, 1993, W. Smith 1981), led T. White (1969, 1976, 1984) to propose the *plant stress hypothesis* (i.e., that stressed plants are more suitable hosts for herbivores). However, experimental studies have indicated that some herbivore species prefer more vigorous plants (G. Waring and Price 1990), leading Price (1991) to propose the alternative *plant vigor hypothe-*

sis. Reviews by Koricheva *et al.* (1998) and G. Waring and Cobb (1992) revealed that response to plant condition varies widely among herbivore species. Schowalter *et al.* (1999) manipulated water supply to creosotebushes, *Larrea tridentata*, in New Mexico and found positive, negative, nonlinear, and nonsignificant responses to moisture availability among the assemblage of herbivore and predator species on this single plant species. These results indicated that both hypotheses can be supported by different insect species on the same plant.

Regardless of the direction of response, water and nutrient subsidy or limitation clearly affect herbivore–plant interactions (Coley *et al.* 1985, M. Hunter and Schultz 1995, Mattson and Haack 1987). Therefore, resource acquisition is moderated, at least in part, by ecosystem processes that affect the availability of water and nutrients (see Chapter 11).

Some plant species respond to increased atmospheric concentrations of CO_2 by allocating more carbon to defenses, such as phenolics or terpenoids, especially if other critical nutrients, such as water or nitrogen, remain limiting (e.g., Arnone *et al.* 1995, Chapin *et al.* 1987, Grime *et al.* 1996, Kinney *et al.* 1997, Roth and Lindroth 1994). However, plant responses to CO_2 enrichment vary considerably among species and as a result of environmental conditions such as light, water, and nutrient availability (Bazzaz 1990, Dudt and Shure 1994, P. Edwards 1989, Niesenbaum 1992), with equally varied responses among herbivore species (e.g., Bezemer and Jones 1998, Salt *et al.* 1996, Watt *et al.* 1995). Such complexity of factors interacting with atmospheric CO_2 precludes general prediction of effects of increased atmospheric CO_2 on insect–plant interactions (Bazzaz 1990, Watt *et al.* 1995).

F. Mechanisms for Exploiting Variable Resources

In a classic paper that stimulated much subsequent research on factors affecting herbivory, Hairston *et al.* (1960) argued that herbivore populations are not limited by food supply because vegetation is normally abundant, and herbivores, when numerous, are able to deplete plant resources. We now know, as described in the preceding text, that plant resources are not equally suitable or acceptable and that herbivore populations often are limited by availability of suitable food. Herbivore populations are regulated by a combination of factors, as discussed in Chapter 6, including dietary toxins. At the same time, insects are capable of feeding on defended hosts. Feeding preferences reflect one mechanism for avoiding defenses. However, insects exhibit a variety of mechanisms for detoxifying, avoiding, or circumventing host defenses.

Herbivorous insects produce a variety of catalytic enzymes, in particular those associated with cytochrome P-450, to detoxify plant or prey defenses (Feyereisen 1999, Karban and Agrawal 2002). Some insects produce salivary enzymes that minimize the effectiveness of plant defenses. Salivary enzymes, such as glucose oxidase applied to feeding surfaces by caterpillars, may inhibit activation of induced defenses (Felton and Eichenseer 1999). Saliva of Heteroptera and Homoptera gels into a sheath that separates the insect's stylet from plant cells, perhaps reducing induced plant responses (Felton and Eichenseer 1999).

Digestive enzymes responsible for detoxification usually are microsomal monooxygenases, glutathione S-transferases, and carboxylesterases (Hung *et al.* 1990) that fragment defensive compounds into inert molecules. Microsomal monooxygenases are a general-purpose detoxification system in most herbivores and have higher activity in generalist species, compared to specialist species or sap-sucking species (Hung *et al.* 1990). More specific digestive enzymes also are produced by some species. Detoxification enzymes can be induced in response to exposure to plant toxins (Karban and Agrawal 2002). For example, caterpillars feeding on diets containing proteinase inhibitors showed reduced function of particular proteinases but responded by producing other proteinases that were relatively insensitive to dietary proteinase inhibitors (Broadway 1995, 1997). The compounds produced through detoxification pathways may be used to meet the insect's nutritional needs (Bernays and Woodhead 1982), as in the case of the sawfly, *Gilpinia hercyniae*, which detoxifies and uses the phenolics from its conifer host (Schöpf *et al.* 1982).

The ability to detoxify plant defenses may predispose many insects to detoxify synthetic insecticides (Feyereisen 1999, Plapp 1976). At least 500 arthropod species are resistant to major insecticides used against them, primarily through a limited number of resistance mechanisms that confer cross-resistance to plant defenses and structurally related toxicants and, in some cases, to chemically unrelated compounds (Soderlund and Bloomquist 1990). Le Goff *et al.* (2003) reported that several cytochrome P-450 genes code for detoxification of DDT (dichlorodiphenyltrichloroethane), imidacloprid, and malathion.

Gut pH is a factor affecting the chelation of nitrogenous compounds by tannins. Some insect species are adapted to digest food at high gut pH to inhibit chelation. The insect thus is relatively unaffected by high tannin contents of its food. Examples include the gypsy moth, feeding on oak, *Quercus* spp., and chrysomelid beetles, *Paropsis atomaria*, feeding on *Eucalyptus* spp. (Feeny 1969, Fox and Macauley 1977).

Sequestration and excretion are alternative means of avoiding the effects of host toxins that cannot be detoxified. Sequestered toxins are transported quickly to specialized storage tissues (the exoskeleton or protected pouches), whereas remaining toxins are transported to the Malphigian tubules for elimination. Sequestered toxins become part of the insect's own defensive strategy (Blum 1981, 1992, Conner *et al.* 2000).

Several mechanisms are used to avoid or circumvent host defensive chemicals. Life history phenology of many species is synchronized with periods of most favorable host nutritional chemistry (Feeny 1970, Varley and Gradwell 1970). Diapause can be an important mechanism for surviving periods of adverse host conditions, as well as adverse climatic conditions. In fact, diapause during certain seasons may reflect seasonal patterns of resource availability more than abiotic conditions. For example, many tropical herbivores become dormant during the dry season when their host plants cease production of foliage or fruit and become active again when production of foliage and fruit resumes in the wet season. Diapause can be prolonged in cases of unpredictable availability of food resources, as in the case of insects feeding on seeds of trees that produce seed crops irregularly. Turgeon *et al.* (1994) reported that 70 species of Diptera, Lepidoptera, and Hymenoptera that feed on conifer cones or seeds can remain in diapause for as long as 7 years. In other words, insect populations often have considerable capacity to survive long periods of unsuitable resource conditions through diapause.

Some herbivores sever the petiole or major leaf veins to inhibit translocation of induced defenses during feeding (Becerra 1994, Karban and Agrawal 2002). Sawflies (Diprionidae) sever the resin canals of their conifer hosts or feed gregariously to consume foliage before defenses can be induced (McCullough and Wagner 1993). Species feeding on plants with photooxidant defenses often feed at night or inside rolled leaves to avoid sunlight (Berenbaum 1987, Karban and Agrawal 2002).

Several aphids and gall-formers have been shown to stimulate plant accumulation of nutrients in colonized tissues. For example, Koyama *et al.* (2004) reported that the amount of amino acids exuding from leaves galled by the aphid *Sorbaphis chaetosiphon* was five times that from ungalled leaves. Furthermore, galls retained high amino acid concentrations throughout April, whereas amino acid concentrations declined rapidly during this period in ungalled leaves. Koyama *et al.* (2004) also compared growth and reproduction of another aphid, *Rhopalosiphum insertum*, which can displace gall aphids or colonize ungalled leaves. Aphid growth and reproduction were significantly higher for colonies experimentally established in galls, compared to colonies established on ungalled leaves, indicating a positive effect of gall formation.

Some insects vector plant pathogens that inhibit host defense or induce favorable nutritional conditions in plant hosts. However, not all insects that vector plant pathogens benefit from host infection (Kluth *et al.* 2002).

Many predaceous insects use their venoms primarily for subduing prey and secondarily for defense. Venoms produced by predaceous Heteroptera, Diptera, Neuroptera, Coleoptera, and Hymenoptera function to paralyze or kill prey (Schmidt 1982), thereby minimizing injury to the predator during prey capture. The carabid beetle, *Promecognathus*, a specialist predator on *Harpaphe* spp. and other polydesmid millipedes, avoids the cyanogenic secretions of its prey by quickly biting through the ventral nerve cord at the neck, inducing paralysis (G. Parsons *et al.* 1991). Nevertheless, host defenses increase handling time and risk of injury and mortality for the consumer (Becerra 1994).

Diversion of limited resources to detoxification enzymes or efforts to circumvent or avoid defenses all involve metabolic costs (Karban and Agrawal 2002, Kessler and Baldwin 2002). Lindroth *et al.* (1991) evaluated the effect of several specific nutrient deficiencies on detoxification enzyme activity in the gypsy moth. They found that larvae on a low-protein diet showed compensatory feeding behavior (although not enough to offset reduced protein intake). Soluble esterase and carbonyl reductase activities increased in response to protein deficiency but decreased in response to vitamin deficiency. Polysubstrate monooxygenase and glutathione transferase activities showed no significant response. Furthermore, Carrière *et al.* (2001b) reported that pink bollworm, *Pectinophora gosypiella*, resistance to transgenic (Bt) cotton was associated with reduced percentage emergence from diapause, compared to nonresistant bollworm, indicating fitness costs of developing resistance strategies.

II. RESOURCE ACCEPTABILITY

The variety of resources and their physical and biochemical properties, including defensive mechanisms, is too great in any ecosystem for any species to exploit all possible resources. The particular physiological and behavioral adaptations of insects to obtain sufficient nutrients and avoid toxic or undigestable materials determine their feeding preferences, i.e., which resources they can or will exploit. Potential resources vary widely in nutritional value. Animal tissues have higher nutritional value than do plant tissues because of the preponderance of indigestible cellulose in plant tissues. Nutritional quality of foliage is higher than that of root tissue. Nutritional value varies between bark, sapwood and heartwood tissues (Hodges *et al.* 1968, Schowalter *et al.* 1998). In fact, exploitation of sapwood requires mutualistic interaction with fungi or bacteria, or other adaptations, to acquire sufficient nutrients from a resource that is largely indigestible cellulose (Ayres *et al.* 2000, see Chapter 8). Insects specialized to exploit particular physical and chemical conditions often lose their ability to exploit other resources. Even species that feed on a wide variety of resource types (e.g., host species) are limited in the range of resources they can exploit. For example, the variety of plant species (representing many plant families) eaten by gypsy moth share primarily phenolic defenses; plants with terpenoid or alkaloid defenses usually are not exploited (J. Miller and Hansen 1989).

Particular compounds can be effective defenses against nonadapted herbivores and, at the same time, be phagostimulants for adapted herbivores (Shonle and Bergelson 2000). For example, Tallamy *et al.* (1997) reported that cucurbitacins (bitter triterpenes characterizing the Cucurbitaceae) deter feeding and oviposition by nonadapted mandibulate insect herbivores but stimulate feeding by haustellate insect herbivores.

Malcolm (1992) identified three types of consumers with respect to a chemically defended prey species. Excluded predators cannot feed on the chemically defended prey, whereas included predators can feed on the chemically defended prey with no ill effect. Peripheral predators experience growth loss, etc., when fed chemically defended prey as a result of the effects of the defensive chemicals on predator physiology or on the nutritional quality of the prey. The effectiveness of peripheral predators on prey differing in chemical defense may be a key to understanding the ecology and evolution of predator–prey interactions. Feeding preferences generally depend on three integrated factors: resource quality, susceptibility, and acceptability.

Resource quality, as described in the preceding text, represents the net nutritional value of the resource as determined by the nutrients available to the insect less the energy and resources needed to detoxify or avoid defenses. Just as production of defensive compounds is expensive for the host in terms of energy and resources, production of detoxification enzymes or development of avoidance mechanisms is expensive in terms of energy, resources, time searching, and exposure to predators. Some of the nutrients in the food must be allocated to production of detoxification enzymes or to energy expended in searching for more suitable food. Although diversion of dietary N to production of detoxification enzymes should be reduced if N is limiting, Lindroth *et al.* (1991) found little change in detoxification enzyme activity in response to nutrient deficiencies in gypsy moth larvae. However, defenses can have beneficial side effects for the consumer. M. Hunter and Schultz (1993) reported that phenolic defenses in oak leaves reduced susceptibility of gypsy moth larvae to nuclear polyhedrosis virus.

Resource susceptibility represents the physiological condition of the host, whether for herbivores or predators. Injury or adverse environmental conditions can stress organisms and impair their ability to defend themselves. Initially, stress may prevent expression of induced defenses, an added cost, or may prevent production of constitutive defenses but allow induction of defenses, as needed. Nitrogen limitation may prevent production of nitrogenous defenses but increase production of nonnitrogenous defenses. Reduced production of biochemical defenses reduces the cost of detoxification or avoidance to the predator. Hence, specialist species can allocate more energy and resources to growth and reproduction, and generalists may be able to expand their host range as biochemical barriers are removed.

Resource acceptability represents the willingness of the insect to feed, given the probability of finding more suitable resources or in view of other tradeoffs. Most insects have relatively limited time and energy resources to spend searching for food. Hence, marginally suitable resources may become sufficiently profitable when the probability of finding more suitable resources is low, such as in diverse communities composed primarily of nonhosts. Courtney (1985, 1986) reported that oviposition by a pierid butterfly, *Anthocharis cardamines*, among several potential host plant species was inversely related to the suitability of those plant species for larval development and survival (Fig. 3.10). The more suitable host plant species were relatively rare and inconspicuous compared to the less suitable host species. Hence, butterfly fitness was maximized by laying eggs on the most conspicuous (apparent) plants, thereby ensuring reproduction, rather than by risking reproductive failure during continued search for more suitable hosts. Nevertheless, insects forced to feed on less suitable resources show reduced growth and survival rates (Bozer *et al.* 1996, Courtney 1985, 1986).

Insects face an evolutionary choice between maximizing the range of resources exploited (*generalists)* or maximizing the efficiency of exploiting a particular resource (*specialists)*. Generalists maximize the range of resources exploited through generalized detoxification or avoidance mechanisms, such as broad-spectrum microsomal monooxygenases, but sacrifice efficiency in exploiting any particular resource because unique biochemicals reduce digestion or survival (Bowers and Puttick 1988). Generalists may benefit from a mixed diet through dilution of any one host's defensive compounds (Bernays *et al.* 1994) or increase their efficiency by exploiting stressed hosts that have

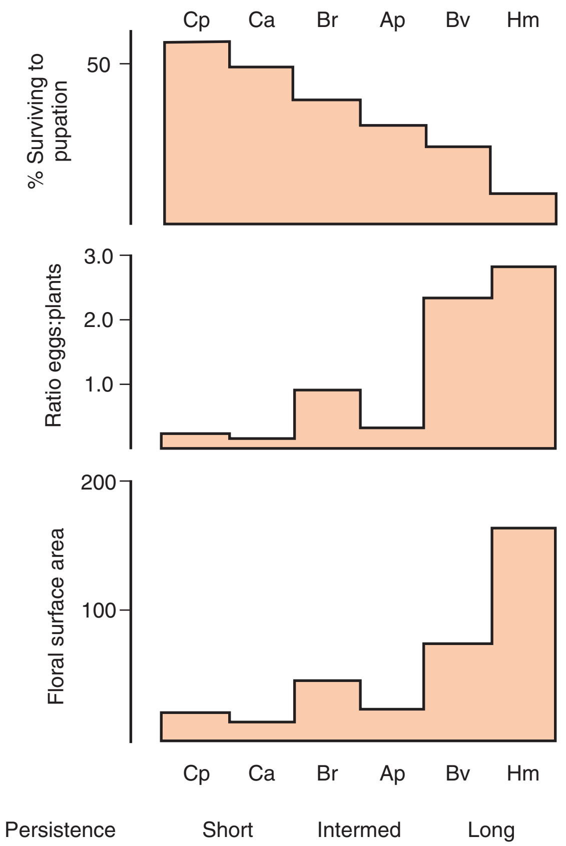


FIG. 3.10 Tradeoff between plant suitability for larval survival (*top*) and efficiency of oviposition site selection by adult pierids, *Anthocharis cardamines,* as indicated by the ratio of eggs per host species (*middle*) and plant apparency (i.e., floral surface area and longevity [*bottom*]). Searching females preferentially oviposit on the most conspicuous plants, although these are not the most suitable food plants for their larvae. Cp, *Cardamine pratensis*; Ca, *C. amara*; Br, *Brassica rapa*; Ap, *Allaria petiolate*; Br, *Barbarea vulgaris*; and Hm, *Hesperis matronalis.* From Courtney (1985) with permission from Oikos.

sacrificed production of defenses. Specialists maximize the efficiency of exploiting a particular host through more specific detoxification or avoidance strategies, minimizing the effect of more of the host's constitutive and induced defenses, but sacrifice ability to feed on other species with different defenses (Bowers and Puttick 1988).

Some generalists that occur over large geographic areas may be more specialized at the local level. Parry and Goyer (2004) demonstrated that forest tent caterpillar, *Malacosoma disstria*, is a composite of regionally specialized populations rather than an extreme generalist. In a reciprocal transplant experiment, tent caterpillars from Louisiana and Michigan, in the United States, and Manitoba, Canada, were reared on the variety of hosts exploited by northern and southern populations. Tent caterpillars from northern populations showed greatest growth and survival on trembling aspen, *Populus tremuloides*, and red oak, *Quercus rubra*, both northern host species, and poorest growth and survival on water tupelo, *Nyssa aquatica*, a southern host species. Tent caterpillars from southern populations showed greatest growth and survival on water tupelo and poorest growth and survival on sugar maple, *Acer saccharum*, a northern host species.

Specialists and generalists contribute to host population dynamics and to community structure and function in different ways, as described in Chapters 6 and 8. Generalists usually exploit more abundant host species and may reduce competition among hosts, but do not effectively target rapidly increasing host populations. By contrast, specialists focus on particular host species and control host population growth more effectively but must be able to discover sparsely distributed hosts.

Searching insects initially identify acceptable hosts. They then select particular host tissues based on nutritional value. Nutritional quality can vary even within tissues. For example, insects may target particular portions of leaves, based on gradients in the ratio among amino acids along the leaf blade (Haglund 1980, K. Parsons and de la Cruz 1980), and particular heights on tree boles, based on gradients in ratios among amino acids and carbohydrates (Hodges *et al.* 1968).

Many insects feed on different resources at different stages of development. Most Lepidoptera feed on plant foliage, stems, or roots as larvae, but many feed on nectar as adults. Some cerambycid beetles feed in wood as larvae but feed on pollen or nectar as adults. A number of Diptera and Hymenoptera have predaceous or parasitic larvae but feed on pollen or nectar resources as adults. Many aphids alternate generations between two host plant species (Dixon 1985). Clearly, these changes in food resources require changes in digestive abilities between life stages. Furthermore, population survival requires the presence of all necessary resources at an appropriate landscape scale.

The primacy of resource exploitation for development and survival places strong selective pressure on insects to adapt to changing host quality. This has led to the so-called "evolutionary arms race," in which herbivory selects for new plant defenses and the new plant defenses select for insect countermeasures. This process has driven reciprocal speciation in both plants and insects, with examples of cladograms of plant species and associated insect species mirroring each other (Becerra 1997). The long exposure of insects to a wide variety of host (especially plant) toxins has led to flexible detoxification and other mechanisms to circumvent those defenses, especially among generalists. This ability to detoxify various plant defenses predisposes many herbivorous species to detoxify synthetic insecticides.

III. RESOURCE AVAILABILITY

The abundance, distribution, and apparency of acceptable resources determine their availability to organisms. Resources are most available when distributed evenly at nonlimiting concentrations or densities. Organisms living under such conditions need not move widely to locate new resources and tend to be relatively sedentary. Microorganisms suspended in a concentrated solution of organic molecules (such as in eutrophic aquatic ecosystems or in decomposing detritus) and filter feeders and scale insects that capture resources from flowing solutions of resources may enjoy relatively nonlimiting resources for many generations.

However, necessary resources usually are less concentrated, available at suboptimal ratios with other resources, or are unevenly distributed at the scale of use by most terrestrial organisms. This requires that organisms select habitats where limiting resources are most concentrated or in most efficient balance and seek new sources as current resources become depleted. Although active searching is facilitated by locomotory ability, plant roots are capable of growing in the direction of more concentrated resources. Insects and other animals use various physiological and behavioral mechanisms to detect, orient toward, and move to concentrations of food.

A. Foraging Strategies

Insect behavior can be viewed from the standpoint of efficiency of resource acquisition and allocation (Sterner and Elser 2002, see also Chapter 4). Foraging should focus on resources that provide the best return and minimum risk for the effort expended. Hence, bumble bees, *Bombus* spp., forage on low-energy resources only at high temperatures when the insects do not require large amounts of energy to maintain sufficiently high body temperature for flight (Bell 1990, Heinrich 1979, 1993). Other host-seeking insects tend to focus their searching where the probability of host discovery is highest (i.e., where hosts are concentrated or most apparent) (Bell 1990, Kareiva 1983).

Foraging theory focuses on optimization of diet, risk, and foraging efficiency (Kamil *et al.* 1987, Schultz 1983, Stephens and Krebs 1986, Townsend and Hughes 1981). Profitable resources provide a gain to the consumer, but nonnutritive or toxic resources represent a cost in terms of time, energy, or nutrient resources expended in detoxification or continued search. Continued search also increases exposure to predators or other mortality agents. Sublethal doses of defensive chemicals reduce nutritional value of the resource, so they should be avoided when resources are abundant but they may be eaten when more profitable resources are unavailable or not apparent (Courtney 1985, 1986). Consumers should maximize foraging efficiency by focusing on patches with high profitability (and ignore low-profitability patches) until their resource value declines below the average for the landscape matrix. Orientation toward cues indicating suitable resources improves the efficiency of food acquisition. Furthermore, learning confers an ability to improve resource acquisition as a result of experience.

Most insects must search for suitable food at some spatial scale. Even within a particular plant, nutritional quality may vary considerably among individual leaves (e.g., between sun and shade leaves, young and old leaves) (Schultz 1983, Whitham 1983). Foraging strategy represents a tradeoff between costs (in terms of reduced growth and survival) of searching, costs of feeding on less suitable food, and costs of exposure to predators.

Schultz (1983) developed a tradeoff surface to illustrate four foraging strategies for arboreal caterpillars (Fig. 3.11). Foraging can be optimized by searching for more nutritive food and risking attention of predators, accepting less nutritive food, or defending against predation. Natural selection can favor a reduction in cost along any of the three axes, within constraints of the other two costs. Feeding selectively on the most suitable food during the day incurs a moderate cost of movement (energy expenditure at higher temperature) and high risk of predation. Selective feeding at night reduces predation risk but increases the energetic cost of movement under cooler temperatures, which then restricts the time spent feeding, especially at high latitudes. Crypsis (camouflage) reduces the risk of predation for day-feeders, but the cost of movement (in terms of attraction of predators) is substantial and limits ability to search for the most suitable food. Conversely, aposomatic (warning) coloration can reduce the risk of predation and allow greater freedom of movement, but the energy expenditure of movement and cost of biochemical sequestration must be considered. Species that mimic, and live on or in, their food can avoid both movement and predation costs but have no choice in their food after initial colonization. Hence, feeding costs may be quite high.

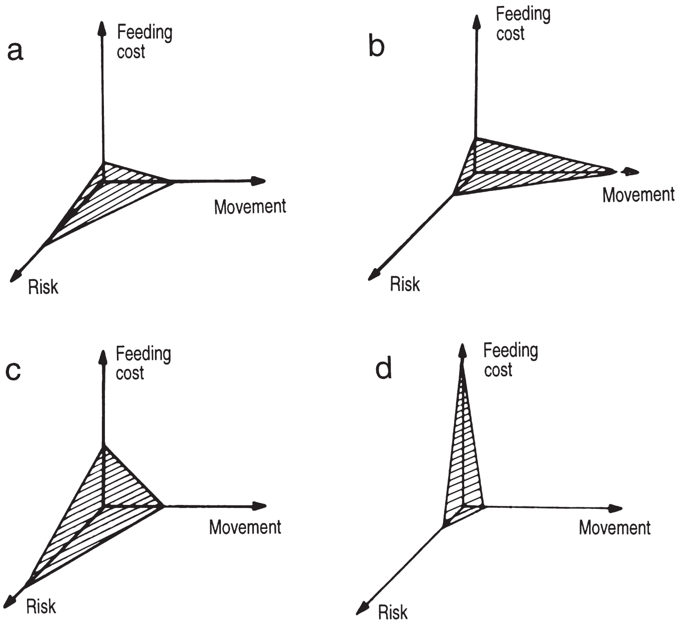


FIG. 3.11 Tradeoff planes of selected caterpillar foraging strategies. Costs of feeding (i.e., metabolic costs of digestion, reduced growth, etc.), movement (metabolic costs of reduced growth), and risks (e.g., probability of capture or reduced growth as a result of time spent hiding) increase in the direction of the arrows: **a:** selective diurnal feeder, **b:** selective nocturnal aposomatic feeder, **c:** diurnal cryptic feeder, and **d:** food mimic. From Schultz (1983). Please see extended permission list pg 569.

Predators also face tradeoffs between hunting, ambush, or intermediate strategies. Hunting requires considerable expenditure of energy searching for prey, but it has a high return, depending on ability to detect prey from a distance. Detection can be increased by orienting toward prey odors or plant odors indicative of prey. Accordingly, many predaceous species are attracted to mating pheromones of their prey (Stephen *et al.* 1993) or to volatile chemicals released by plants in response to herbivory (Turlings *et al.* 1993). Ambushers either sit and wait or use traps to capture prey. As examples, dragonfly larvae hide in the substrate of aquatic habitats and grasp prey coming within reach, antlion larvae excavate conical depressions in loose sandy soil that prevents escape of ants and other insects that wander into the pit, and webspinning spiders construct sticky orb or tangled webs that trap flying or crawling insects. Movement costs are minimal for these species, but prey encounter is uncertain. Frequency of prey encounter can be increased by selecting sites along prey foraging trails, near prey nest sites, etc.

B. Orientation

Some insects forage randomly, eventually (at some risk) discovering suitable resources (Dixon 1985, Raffa *et al.* 1993). However, most insects respond to various cues that indicate the suitability of potential resources. The cues to which searching insects respond may differ among stages in the search process. For example, gross cues, indicative of certain habitats, might initially guide insects to a potentially suitable location. They then respond to cues that indicate suitable patches of resources and finally focus on cues characteristic of the necessary resources (Bell 1990, Mustaparta 1984). Experience at the habitat scale can affect search at finer scales. Insects search longer in patches where suitable resources have been detected than in patches without suitable resources, resulting in gradual increase in population density on hosts (Bell 1990, Risch 1980, 1981, Root 1973, Turchin 1988). Orientation toward cues involves the following steps.

1. *Information Processing*

Several types of information are processed by searching insects. Some cues are nondirectional but alert insects to the presence of resources or initiate search behavior. A nondirectional cue may alter the threshold for response to other cues (cross-channel potentiation) or initiate behaviors that provide more precise information (Bell 1990). For example, flying bark beetles usually initiate search for their host trees only after exhausting their fat reserves. Emerging adults of parasitic wasps gather information about their host from odors emanating from host frass or food plant material associated with the emergence site (Godfray 1994). Wasps emerging in the absence of these cues may be unable to identify potential hosts.

Directional information provides the stimulus to orient in the direction of the perceived resource. For example, detection of attractive chemicals without airflow initiates nondirectional local search, whereas addition of airflow stimulates orientation upwind (Bell 1990). Accuracy of orientation increases with signal intensity. Signal intensity decreases with distance and increases with density of the source (Elkinton *et al.* 1987, M. Stanton 1983). Concentration of attractive odors remains higher at greater distances from patches of high host density compared to patches of low host density (Fig. 3.12). Insects move upwind in circuitous fashion at low vapor concentration, but movement becomes increas-

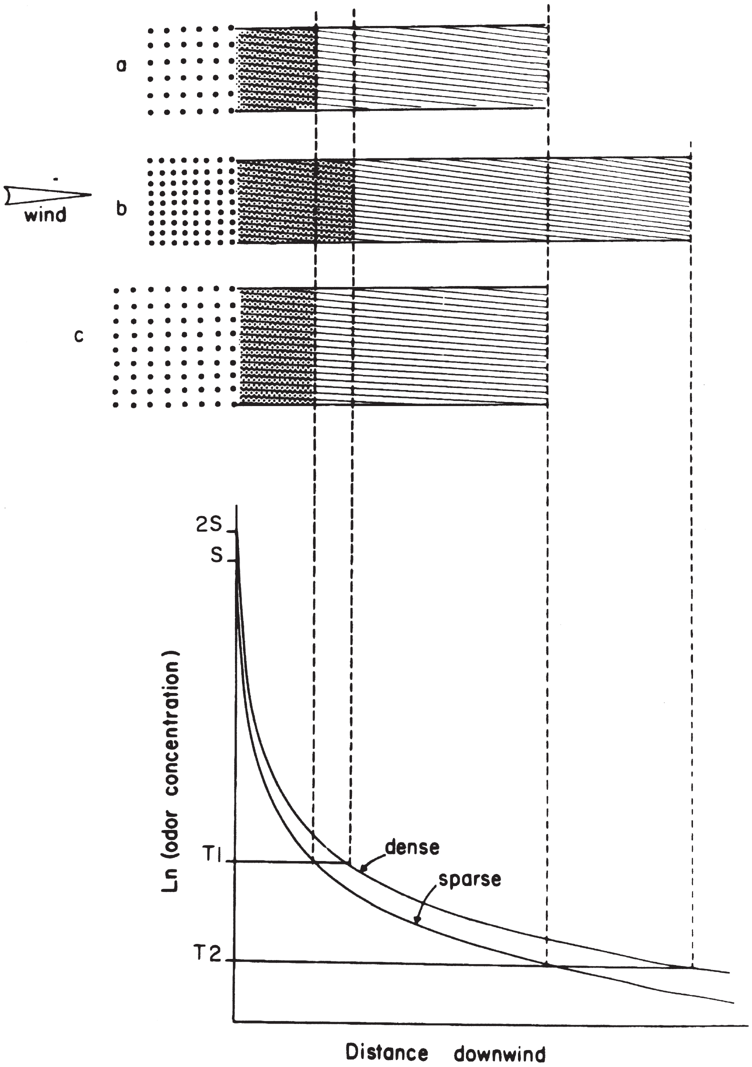


FIG. 3.12 Odor concentration downwind from patches of two host densities: the low-density odor curve represents patches a and c, whereas the high-density curve represents patch b. The curves reflect an ideal situation in which diffusion is overshadowed by convection resulting from wind. In still air, odor concentration cannot be changed by altering host-plant density. Attractive areas shown as rectangles are actually irregular in shape. Attractive zones for low-sensitivity herbivores (threshold T1) are stippled; those for high-sensitivity herbivores (T2) are shaded. From M. Stanton (1983).

ingly directed as vapor concentration increases upwind (Cardé 1996). Insects integrate visual, chemical, and acoustic signals to find their resources, switching from less precise to more precise signals as these become available (Bell 1990).

2. Responses to Cues

Visual cues include host silhouettes and radiant energy. Some species find arboreal resources by orienting toward light. Aphids are attracted to young, succulent foliage and to older senescent foliage by longer-wavelength yellow, but this cue is not a good indicator of host species (Dixon 1985). Aphids, *Pemphigus betae*, migrating in autumn may discriminate among susceptible and resistant poplar trees on the basis of prolonged leaf retention by more susceptible hosts (N. Moran and Whitham 1990). Many bark beetles are attracted to dark-colored silhouettes of tree boles and can be attracted to other cylindrical objects or prevented from landing on tree boles painted white (Goyer *et al.* 2004, Strom *et al.* 1999). Some parasitic wasps detect their wood-boring hosts by means of infrared receptors on their antennae (Matthews and Matthews 1978).

The importance of flower color and color patterns to attraction of pollinators has been a topic of considerable research (Chittka and Menzel 1992, Heinrich 1979, Wickler 1968). Reds and blues are more easily detected in open or well-lit ecosystems; hence they are more common in tropical and grassland ecosystems, white is more readily detected under low-light conditions, such as in the understories of forests. Ultraviolet designs, detectable by insects, provide important cues to insect pollinators. Insects can detect ultraviolet "runways" or "nectar guides" that guide the insect to the nectaries (Eisner *et al.* 1969, Heinrich 1979, Matthews and Matthews 1978). Some floral designs in the orchid genus *Ophrys* resemble female bees or wasps and produce odors similar to the mating pheromones of these insects. Male bees or wasps are attracted and unwittingly pollinate these flowers while attempting to copulate (Wickler 1968).

Nonhosts that are visually similar to hosts can interfere with host discovery by insects that rely on visual cues. For example, Hambäck *et al.* (2003) reported that leaf-feeding beetles, *Galerucella* spp., were significantly less abundant on purple loosestrife, *Lythrum salicaria*, that were surrounded by nonhost or artificial shrubs than on hosts that were not surrounded by nonhost or artificial shrubs.

Many plant chemicals are highly volatile and are the basis for floral and other plant odors. Prominent among these are the monoterpenes, such as verbenone in verbena flowers and alpha-pinene in conifers, and aromatic compounds, such as vanillin (Harborne 1994). These represent attractive signals to pollinators and to herbivores adapted to feed on a particular plant. Some odors repel some insects. For example, verbenone and 4-allylanisole, in the resin of various trees, repel some bark beetle species (Hayes *et al.* 1994). Verbenone is present in the bark of certain conifers (including western redcedar, *Thuja plicata*, and Pacific silver fir, *Abies amabilis*) and likely influences orientation by bark beetles among tree species in diverse forests (Schowalter *et al.* 1992). Nonattractive or repellent odors from nonresources can mix with attractive odors in the airstream of more diverse ecosystems and disrupt orientation (Fig. 3.13). For example, volatile

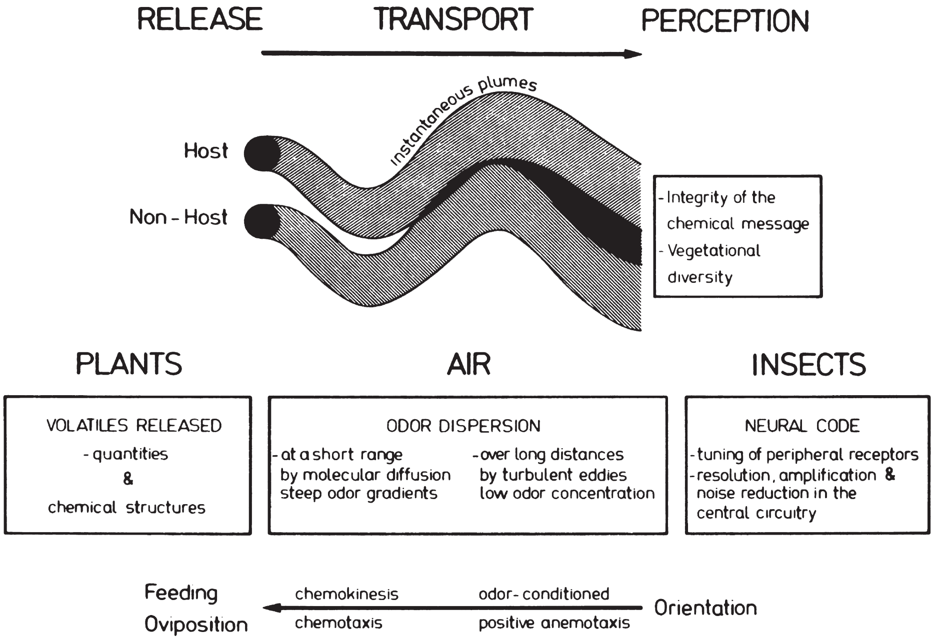


FIG. 3.13 Elements of host odor perception in insects. From Visser (1986) with permission from the Annual Review of Entomology, Vol. 31, © 1986 by Annual Reviews. Please see extended permission list pg 569.

chemicals from nonhost angiosperms disrupted attraction of spruce beetles, *Dendroctonus rufipennis*, and western pine beetle, *D. brevicomis,* to host conifer odors (Poland *et al.* 1998). However, not all insects attracted to host odors suffer disruption by nonhost odors (Hambäck *et al.* 2003).

Predators often are attracted to prey pheromones or odors from damaged plants that indicate the presence of prey (Kessler and Baldwin 2001, Stephen *et al.* 1993, Turlings *et al.* 1990, 1993, 1995). Pheromones are known from more than 1000 insect species (Mustaparta 2002).

Attractiveness of volatile biochemicals to insects is species specific (Mustaparta 1984). A chemical that is attractive to one species may be unattractive or even repellent to other, even related, species. For example, among sympatric *Ips* species in California, *I. pini* and *I. paraconfusus* both are attracted to ipsdienol, but *I. paraconfusus* also incorporates ipsenol and cis-verbenol in its pheromone blend, whereas *I. latidens* is attracted to ipsenol and cis-verbenol but not in the presence of ipsdienol (Raffa *et al.* 1993). Plants that depend on dipteran pollinators often produce odors that resemble those of carrion or feces to attract these insects. Peakall and Beattie (1996) and Peakall *et al.* (1987) described pollination of Australian orchids by male ants and wasps during pseudocopulation, suggesting that the chemical stimulus is similar to the mating pheromone produced by potential mates. Sex pheromones (see Chapter 4) often are more attractive when mixed with host volatiles (e.g., Raffa *et al.* 1993), indicating prior discovery and evaluation of suitable hosts.

Studies have shown that detection of relevant odors is genetically encoded but response can be modified through learning (see the following section). Insects have a relatively simple nervous system, composed of receptor neurons that detect chemical signals, interneurons that integrate and convey information, and motor neurons that elicit the behavioral response. Olfactory receptor neurons are located in various sensilla, primarily on the antennae. Volatile chemicals apparently diffuse through the cuticle and bind to receptor proteins that are highly selective for biologically relevant molecules (Mustaparta 2002). These proteins transport the odor molecule to a neuronal membrane that contains receptor proteins genetically coded for specific molecules; each receptor neuron expresses proteins specific to certain odor molecules. Therefore, the discrimination power of an organism depends on the number of different neuron types (Mustaparta 2002).

Once a chemical attractant is detected in the air or water current, the insect begins a circuitous search pattern that involves continually turning in the direction of increasing odor concentration (Cardé 1996). However, insects following the odor trail, or plume, are far from assured of reaching the source. Odor plumes often are disrupted by turbulence, resulting from habitat heterogeneity (e.g., substrate or canopy irregularities) (Mafra-Neto and Cardé 1995, Murlis *et al.* 1992). For example, Fares *et al.* (1980) found that openings in forest canopies created sites of soil warming and convective eddies that dissipated chemical plumes. Elkinton *et al.* (1987) found that male gypsy moth response to a caged female declined from 89% at 20 m distance to 65% at 120 m. Of those that responded, arrival at the female's cage declined from 45% at 20 m to 8% at 120 m (see Chapter 4).

If an insect successfully arrives at the source of attractive cues, it engages in close-range gustatory, olfactory, or sound reception (Dixon 1985, Raffa *et al.* 1993, Städler 1984). Contact chemoreceptive sensilla generally have a single pore at the tip, with unbranched dendrites from 2–10 receptor cells (R. Chapman 2003, E. Städler 1984) and are located on antennae, mouthparts, or feet (Dixon 1985, E. Städler 1984). These sensors provide information about nutritive value and defensive chemistry of the resource (R. Chapman 2003, Raffa *et al.* 1993). Certain plant chemicals act as phagostimulants or as deterrents (R. Chapman 2003). For example, cucurbitacins (the bitter triterpenes common to Cucurbitaceae) deter feeding and oviposition by nonadapted mandibulate insects but are phagostimulants for diabroticine chrysomelid beetles (Tallamy and Halaweish 1993). Predators also may avoid prey containing toxic or deterrent chemicals (Stamp *et al.* 1997, Stephens and Krebs 1986). Many parasitic wasps avoid hosts marked by wasps that oviposited previously in that host (Godfray 1994). Because hosts support only a limited number of parasitoid offspring, often no more than one, avoidance of previously parasitized hosts reduces competition among larvae within a host.

Acoustic signals include the sounds produced by cavitating plant cells and by potential mates. Water-stressed plants often produce audible signals from the collapse of cell walls as turgor pressure falls (Mattson and Haack 1987). Cavitation thus is a valuable cue to stressed, and potentially more suitable, plants. Attraction to this signal may partly explain the association of bark beetles with water-stressed trees (Mattson and Haack 1987, Raffa *et al.* 1993).

3. Attraction of Conspecific Insects

Insects also can signal the presence of suitable resources to conspecific insects. Such cooperation increases opportunities for acquisition of shared resources or larger prey and improves mating success (see Chapter 4).

Acoustic signals (stridulation) from potential mates, especially if combined with attractive host cues, advertise discovery and evaluation of suitable resources. Stridulation contributes to optimal spacing and resource exploitation by colonizing bark beetles (Raffa *et al.* 1993, Rudinsky and Ryker 1976).

Attractive and repellent chemicals produced by insects (pheromones) also advertise the location of suitable resources and potential mates (Fry and Wehner 2002, Raffa *et al.* 1993, Rudinsky and Ryker 1976). Most insects produce pheromones, but those of Lepidoptera, bark beetles, and social insects have been studied most widely. Social insects produce recognition pheromones that distinguish colony members from noncolony members and trail pheromones that are deposited along foraging trails to guide other members of a colony to food resources and back to the colony (B. Smith and Breed 1995, Traniello and Robson 1995). Trail pheromones also are used by tent caterpillars (Fitzgerald 1995).

A variety of chemical structures are used to mark trails (Fig. 3.14). A plant-derived monoterpene, geraniol, is obtained from flower scents, concentrated, and used by honey bees, *Apis mellifera*, to mark trails and floral resources (Harborne 1994). Trail markers can be highly effective. The trail marker produced by the leaf-cutting ant, *Atta texana*, is detectable by ants at concentrations of 3.48×10^8 molecules cm^{-1}, indicating that 0.33 mg of the pheromone would be sufficient to mark a detectable trail around the world (Harborne 1994). Although trail markers were once thought to be species specific, more recent work has shown that multiple species may use the same compounds as trail markers, with varying degrees of interspecific recognition (Traniello and Robson 1995). Furthermore, synthetic analogues (e.g., 2-phenoxyethanol) also may elicit trail-following behavior, despite little structural similarity to natural trail markers (J. Chen *et al.* 1988).

Von Frisch (1967) pioneered study of the sophisticated communication used by honey bees. The elaborate movements of the "bee dance" communicate distance and direction to suitable resources to other foragers (F. Dyer 2002).

C. Learning

Insects can increase their efficiency of acquiring suitable resources over time as a result of learning. Learning is difficult to demonstrate because improved performance with experience often may result from maturation of neuromuscular systems rather than from learning (Papaj and Prokopy 1989). Although an unambiguous definition of learning has eluded ethologists, a simple definition involves any repeatable and gradual improvement in behavior resulting from experience (Papaj and Prokopy 1989, Shettleworth 1984). From an ecological viewpoint, learning increases the flexibility of responses to variation in resource availability

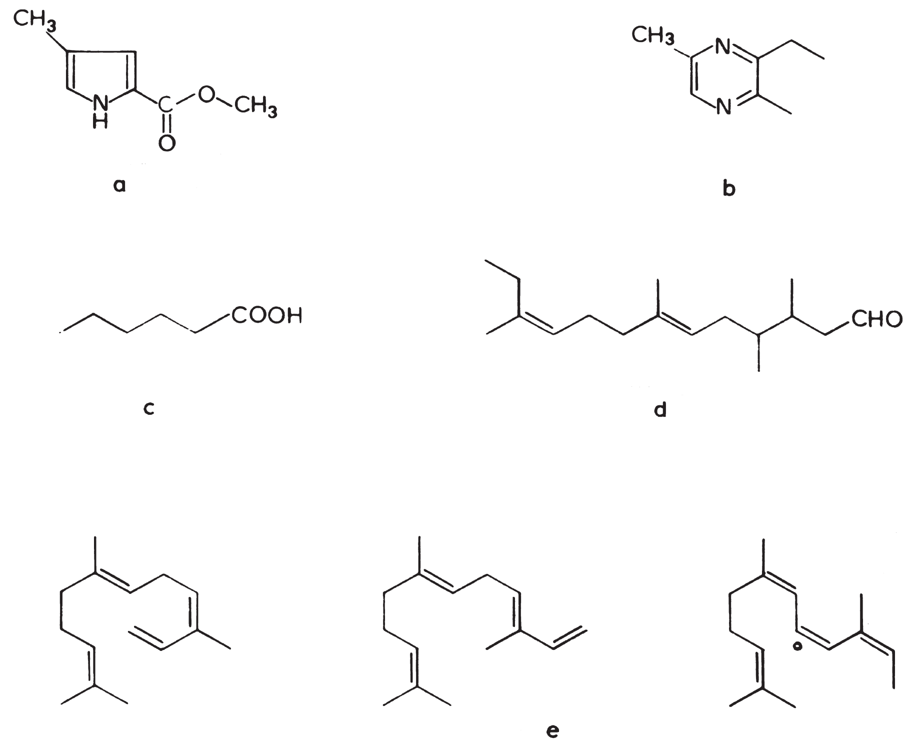


FIG. 3.14 Trail pheromones of myrmicine ants. **a:** *Atta texana* and *A. cephalotes*, **b:** *A. sexdens rubropilosa* and *Myrmica* spp., **c:** *Lasius fuliginosus*, **d:** *Monomorium pharaonis*, and **e:** *Solenopsis invicta*. From Bradshaw and Howse (1984) with permission from Chapman and Hall.

and may be most adaptive when short-term variation is low but long-term variation is high (Stephens 1995).

Learning by insects has been appreciated less widely than has learning by vertebrates, but a number of studies over the past half century have demonstrated learning by various insect groups (cf., Cunningham *et al.* 1998, Daly *et al.* 2001, Drukker *et al.* 2000, Gong *et al.* 1998, J. Gould and Towne 1988, A. Lewis 1986, Meller and Davis 1996, Papaj and Lewis 1993, Raubenheimer and Tucker 1997, Schneirla 1953, von Frisch 1967, Wehner 2003). Schneirla (1953) was among the first to report that ants can improve their ability to find food in a maze. However, the ants learned more slowly and applied experience less efficiently to new situations than did rats. Learning is best developed in the social and parasitic Hymenoptera and in some other predaceous insects. Nonetheless, learning also has been demonstrated in phytophagous species representing six orders (R. Chapman and Bernays 1989, Papaj and Prokopy 1989). Several types of learning by insects have been identified: habituation, imprinting, associative learning, observational learning, and even cognition.

Habituation is the loss of responsiveness to an unimportant stimulus as a result of continued exposure. Habituation may be the mechanism that induces parasitoids to emigrate from patches that are depleted of unparasitized hosts (Papaj and Prokopy 1989). Although host odors are still present, a wasp is no longer responsive to these odors. Habituation to deterrent chemicals in the host plant may be a mechanism underlying eventual acceptance of less suitable host plants by some insects (Papaj and Prokopy 1989).

Imprinting is the acceptance of a particular stimulus in a situation in which the organism has an innate tendency to respond. Parasitic wasps may imprint on host or plant stimuli at the site of adult emergence. Odors from host frass or the host's food plant present at the emergence site offer important information used by the emerging wasp during subsequent foraging (W. Lewis and Tumlinson 1988). A number of studies have demonstrated that if the parasitoid is removed from its cocoon or reared on an artificial diet, it may be unable to learn the odor of its host or its host's food plant and hence be unable to locate hosts (Godfray 1994).

Associative learning is the linking of one stimulus with another, based on a discerned relationship between the stimuli. Most commonly, the presence of food is associated with cues consistently associated with food. Godfray (1994) summarized a number of examples of associative learning among parasitic Hymenoptera. Information gathered during searching contributes to increased efficiency of host discovery (W. Lewis and Tumlinson 1988). Searching wasps learn to associate host insects with plant odors, including odors not induced by herbivory (Fukushima *et al.* 2002). Subsequently, they preferentially search similar microhabitats (Godfray 1994, Steidle 1998). However, exposure to new hosts or hosts in novel habitats can lead to increased responsiveness to the new cues. Bjorksten and Hoffmann (1998) reported that such learned stimuli can be retained (remembered) for at least 5 days.

Bisch-Knaden and Wehner (2003) demonstrated that desert ants, *Cataglyphis fortis*, learned to associate local foraging trail vectors with individual cylindrical landmarks during homebound runs but not during outbound runs. However, ants returning to the nest initially reverse the outbound vector, then start a systematic search for the nest, indicating that these ants cannot learn separate inbound and outbound vectors that are not 180-degree reversals and that recalibration during homebound runs is dominated by the outbround vector (Wehner *et al.* 2002). Ants are thus able to reach the nest along the shortest route and later return to the food source by 180-degree vector reversal.

Classical conditioning involves substitution of one stimulus for another. Laboratory studies have demonstrated classical conditioning in parasitic wasps. These insects respond to empty food trays after learning to associate food trays with hosts or respond to novel odors after learning to associate them with provision of hosts (Godfray 1994).

Operant conditioning, or trial-and-error learning, is associative learning in which an animal learns to associate its behavior with reward or punishment and then tends to repeat or avoid that behavior accordingly. Association of ingested food with postingestion malaise often results in subsequent avoidance of that food (R. Chapman and Bernays 1989, Papaj and Prokopy 1989). For example, laboratory experiments by Stamp (1992) and Traugott and Stamp (1996) demonstrated that predatory wasps initially attack caterpillars that sequester plant

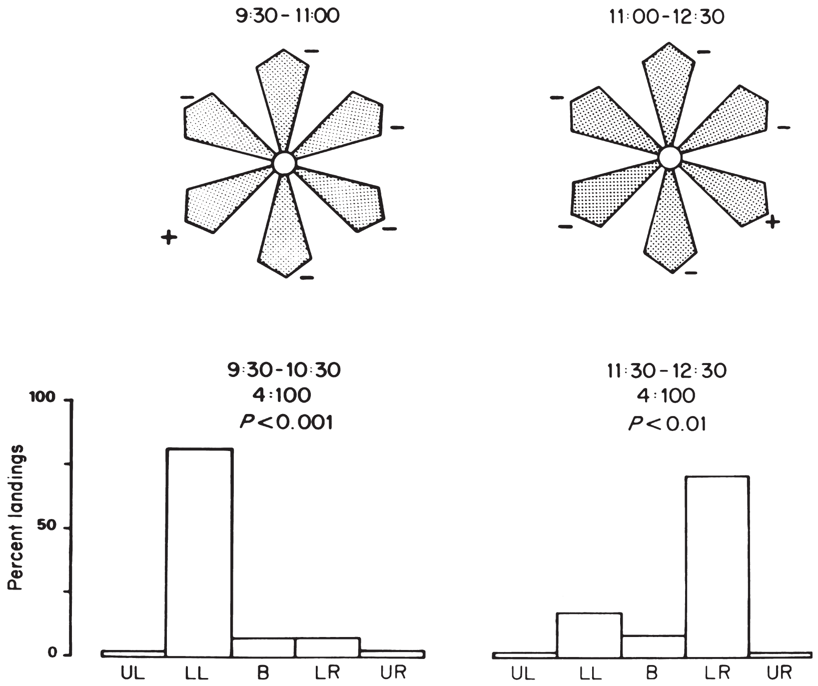


FIG. 3.15 Honey bees can remember how to approach specific flowers in relation to the time of day. Bees trained to land at different positions (+) of an artificial flower at different times in the morning subsequently preferred to land on the petal on which they were trained during the same part of the morning. From J. Gould and Towne (1988).

defenses, but after a few days they will reject unpalatable prey. Honey bees, trained to approach a particular flower from different directions at different times of day, will subsequently approach other flowers from the direction appropriate to the time of day at which rewards were provided during training (Fig. 3.15). Fry and Wehner (2002) and Horridge (2003) found that honey bees can distinguish pattern and landmark orientations and are able to return to food resources even when associated landmark orientation is altered. A. Lewis (1986) reported that cabbage white butterflies became more efficient at obtaining floral rewards by selectively foraging on a particular floral type based on experience. Such floral fidelity can increase pollination efficiency (see Chapter 13). However, improved nectar foraging on larval food plants may increase the likelihood that females will use the same plant for nectar foraging and oviposition (Cunningham *et al.* 1998, 1999).

Insects are capable of complex associative learning. Raubenheimer and Tucker (1997) trained locust, *Locusta migratoria*, nymphs to distinguish between food containers, differing in color, with synthetic diet deficient in either protein or carbohydrate. The locusts were forced to feed from both containers in the arena to obtain a balanced diet. The nymphs subsequently were deprived of either protein or carbohydrate and tested for ability to acquire the deficient nutrient. Locusts significantly more frequently selected food containers of the color previously associated with the deficient nutrient, regardless of color or whether the nutrient was protein or carbohydrate. Wäckers *et al.* (2002) demonstrated that parasitoid wasps, *Microplitis croceipes*, could learn multiple tasks representing feeding and reproduction. Stach *et al.* (2004) found that honey bees can learn multiple conditioning patterns and generalize their response to novel stimuli based on linkage among conditioned stimuli.

Observational learning occurs when animals gather information and modify their behavior in response to observation of other individuals. Observational learning is epitomized by social bees that communicate the location of rich floral resources to other members of the colony through the "bee dance" (F. Dyer 2002, J. Gould and Towne 1988, von Frisch 1967). Movements of this dance, oriented with reference to the sun, inform other foragers of the direction and distance to a food source.

Cognition, characterized by awareness, memory, and judgment, can be demonstrated by application of information gathered during previous experiences to performance in novel situations. This basic form of thinking is widely associated with higher vertebrates. However, J. Gould (1986) demonstrated that honey bees are capable of constructing cognitive maps of their foraging area. Bees were trained to forage at either of two widely separated sites, then captured at the hive and transported in the dark to an unfamiliar site, the same distance from the hive but in a different direction, within a complex foraging area (open areas interspersed with forest). If released bees were disoriented or could not accommodate a sudden change in landmarks, they should fly in random directions. If they have only route-specific landmark memory and were familiar with a foraging route to their release point, they should be able to return to the hive and from there fly to their intended destination (site to which they had been trained). Only if bees are capable of constructing true cognitive maps should they be able to fly from the release point directly to their intended destination. J. Gould (1986) found that all bees flew directly to their intended destinations. Although some studies indicate limits to large-scale cognitive mapping by bees (Dukas and Real 1993, Menzel *et al.* 1998), substantial evidence indicates that honey bees construct and maintain at least local metric spatial representation, referenced to the time of day and to landmarks and line angles to floral resources (J. Gould 1985, 1986, J. Gould and Towne 1988). Wei *et al.* (2002) further demonstrated that honey bees intensively examine the area around a food source through "learning flights." Bees turn back and face the direction of the food source and surrounding landmarks, then circle around, before returning to the hive. The duration of learning flights increases with the sugar concentration of food and the visual complexity of the surrounding landmarks and is longer following initial discovery of food than during subsequent reorientation. These results indicate that bees adjust learning effort in response to the need for visual information. Such advanced learning greatly facilitates the efficiency with which resources can be acquired.

IV. SUMMARY

Insects, as do all organisms, must acquire energy and material resources to synthesize the organic molecules necessary for life processes of maintenance, growth, and reproduction. Dietary requirements reflect the size and life stage of the insect and the quality of food resources. Insects exhibit a variety of physiological and behavioral strategies for finding, evaluating, and exploiting potential resources.

Defensive chemistry of plants and insects affects their quality as food and is a basis for host choice by herbivorous and entomophagous insects, respectively. Nutritional value of resources varies among host species, among tissues of a single organism, and even within tissues of a particular type. Production of defensive chemicals is expensive in terms of energy and nutrient resources and may be sacrificed during unfavorable periods (such as during water or nutrient shortages or following disturbances) to meet more immediate metabolic needs. Such hosts become more vulnerable to predation. Insect adaptations to detoxify or otherwise circumvent host defenses determine host choice and range of host species exploited. Generalists exploit a relatively broad range of host species but exploit each host species rather inefficiently, whereas specialists are more efficient in exploiting a single or a few related hosts that produce similar chemical defenses.

Chemicals also communicate the availability of food and provide powerful cues that influence insect foraging behavior. Insects are capable of detecting food resources over considerable distances. Perception of chemical cues that indicate availability of hosts is influenced by concentration gradients in air or water, environmental factors that affect downwind or downstream dispersion of the chemical, and sensitivity to particular odors. Orientation to food resources over shorter distances is affected by visual cues (such as color or pattern) and acoustic cues (such as stridulation). Once an insect finds a potential resource, it engages in tasting or other sampling behaviors that permit evaluation of resource acceptability.

Efficiency of resource acquisition may improve over time as a result of learning. Although much of insect behavior may be innate, learning has been documented for many insects. Ability to learn among insects ranges from simple habituation to continuous unimportant stimuli, to widespread associative learning among both phytophagous and predaceous species, to observational learning and even cognitive ability. Learning represents the most flexible means of responding to environmental variation and allows many insects to adjust to changing environments during short lifetimes.

4

Resource Allocation

- **I. Resource Budget**
- **II. Allocation of Assimilated Resources**
  - *A. Resource Acquisition*
  - *B. Mating Activity*
  - *C. Reproductive and Social Behavior*
  - *D. Competitive, Defensive, and Mutualistic Behavior*
- **III. Efficiency of Resource Use**
  - *A. Factors Affecting Efficiency*
  - *B. Tradeoffs*
- **IV. Summary**

INSECTS ALLOCATE ACQUIRED RESOURCES IN VARIOUS WAYS, DEPENDING on the energy and nutrient requirements of their physiological and behavioral processes. In addition to basic metabolism, foraging, growth, and reproduction, individual organisms also allocate resources to pathways that influence their interactions with other organisms and abiotic nutrient pools (Elser *et al*. 1996).

It is interesting that much of the early data on energy and nutrient allocation by insects was a byproduct of studies during 1950 to 1970 on anticipated effects of nuclear war on radioisotope movement through ecosystems (e.g., Crossley and Howden 1961, Crossley and Witkamp 1964). Research also addressed effects of radioactive fallout on organisms that affect human health and food supply. Radiation effects on insects and other arthropods were perceived to be of special concern because of the recognized importance of these organisms to human health and crop production. Radioactive isotopes, such as ^{31}P, ^{137}Cs (assimilated and allocated as is K), and ^{85}Sr (assimilated and allocated as is Ca), became useful tools for tracking the assimilation and allocation of nutrients through organisms, food webs, and ecosystems.

I. RESOURCE BUDGET

The energy or nutrient budget of an individual can be expressed by the equation

$$I = P + R + E$$

in which I = consumption, P = production, R = respiration, E = egestion, and I – E = P + R = assimilation. Energy is required to fuel metabolism, so only part of the assimilated energy is available for growth and reproduction (Fig. 4.1). The remainder is lost through respiration. Insects and other heterotherms require little energy to maintain thermal homeostasis. Hence, arthropods generally

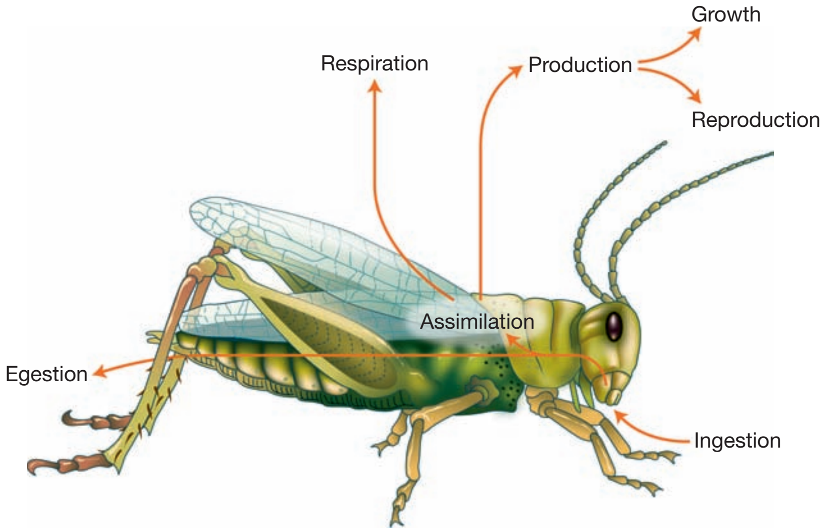


FIG. 4.1 Model of energy and nutrient allocation by insects and other animals. Ingested food is only partially assimilable, depending on digestive efficiency. Unassimilated food is egested. Assimilated food used for maintenance is lost as carbon and heat energy; the remainder is used for growth and reproduction.

respire only 60–90% of assimilated energy, compared to >97% for homeotherms (Fitzgerald 1995, Golley 1968, Phillipson 1981, Schowalter *et al.* 1977, Wiegert and Petersen 1983). Availability of some nutrients can affect an organism's use of others (e.g., acquisition and allocation pathways may be based on differences in ratios among various nutrients between a resource and the needs of an organism) (Elser *et al.* 1996, Holopainen *et al.* 1995, see Chapter 3). *Ecological stoichiometry* has become a useful approach to account for mass balances among multiple nutrients as they flow within and among organisms (Elser and Urabe 1999, Sterner and Elser 2002).

Arthropods vary considerably in their requirements for, and assimilation of, energy and various nutrients. Reichle *et al.* (1969) and Gist and Crossley (1975) reported significant variation in cation accumulation among forest floor arthropods, and Schowalter and Crossley (1983) reported significant variation in cation accumulation among forest canopy arthropods. Caterpillars and sawfly larvae accumulated the highest concentrations of K and Mg, spiders accumulated the highest concentrations of Na among arboreal arthropods (Schowalter and Crossley 1983), and millipedes accumulated the highest concentrations of Ca among litter arthropods (Reichle *et al.* 1969, Gist and Crossley 1975).

Assimilation efficiency (A/I) also varies among developmental stages. Schowalter *et al.* (1977) found that assimilation efficiency of the range caterpillar, *Hemileuca oliviae*, declined significantly from 69% for first instars to 41% for the prepupal stage (Table 4.1). Respiration by pupae was quite low, amounting to only a few percent of larval production. This species does not feed as an adult, so resources acquired by larvae must be sufficient for adult dispersal and reproduction.

TABLE 4.1 Assimilation efficiency, A/I, gross production efficiency, P/I, and net production efficiency, P/A, for larval stages of the saturniid moth, *Hemileuca oliviae*. Means underscored by the same line are not significantly different ($P > 0.05$).

Instar	1	2	3	4	5	6	7	Total
A/I	0.69	0.64	0.60	0.55	0.48	0.43	0.41	0.54
P/I	0.41	0.26	0.28	0.22	0.25	0.26	0.20	0.23
P/I	0.59	0.43	0.47	0.42	0.56	0.63	0.53	0.52

Reproduced from Schowalter *et al.* (1977) with permission from Springer-Verlag.

II. ALLOCATION OF ASSIMILATED RESOURCES

Assimilated resources are allocated to various metabolic pathways. The relative amounts of resources used in these pathways depend on stage of development, quality of food resources, physiological condition, and metabolic demands of physiological processes (such as digestion and thermoregulation), activities (such as foraging and mating), and interactions with other organisms (including competitors, predators, and mutualists). For example, many immature insects are relatively inactive and expend energy primarily for feeding and defense, whereas adults expend additional energy and nutrient resources for dispersal and reproduction. Major demands for energy and nutrient resources include foraging activity, mating and reproduction, and competitive and defensive behavior.

A. Resource Acquisition

Foraging activity is necessary for resource acquisition. Movement in search of food requires energy expenditure. Energy requirements vary among foraging strategies, depending on distances covered and the efficiency of orientation toward resource cues. Hunters expend more energy to find resources than do ambushers. The defensive capabilities of the food resource also require different levels of energy and nutrient investment. As described in Chapter 3, defended prey require production of detoxification enzymes or expenditure of energy during capture. Alternatively, energy must be expended for continued search if the resource cannot be acquired successfully.

Larger animals travel more efficiently than do smaller animals, expending less energy for a given distance traversed. Hence, larger animals often cover larger areas in search of resources. Flight is more efficient than walking, and efficiency increases with flight speed (Heinrich 1979), enabling flying insects to cover large areas with relatively small energy reserves. Dispersal activity is an extension of foraging activity and also constitutes an energy drain. Most insects are short-lived, as well as energy-limited, and maximize fitness by accepting less suitable, but available or apparent, resources in lieu of continued search for superior resources (Courtney 1985, 1986, Kogan 1975).

The actual energy costs of foraging have been measured rarely. Fewell *et al.* (1996) compared the ratios of benefit to cost for a canopy-foraging tropical ant, *Paraponera clavata*, and an arid-grassland seed-harvesting ant, *Pogonomyrmex occidentalis*. They found that the ratio ranged from 3.9 for nectar foraging *P. clavata* and 67 for predaceous *P. clavata* to > 1000 for granivorous *P. occidentalis* (Table 4.2). Differences were a result of the quality and amount of the resource, the distance traveled, and the individual cost of transport. In general, the smaller *P. occidentalis* had a higher ratio of benefit to cost because of the higher energy return of seeds, shorter average foraging distances, and lower energy cost m^{-1} traveled. The results indicated that *P. clavata* colonies have similar daily rates of energy intake and expenditure, potentially limiting colony growth, whereas *P. occidentalis* colonies have a much higher daily intake rate, compared to expenditure, reducing the likelihood of short-term energy limitation.

Insects produce a variety of biochemicals to exploit food resources. Trail pheromones provide an odor trail that guides other members of a colony to food resources and back to the colony (see Fig. 3.14). Insects that feed on chemically defended food resources often produce more or less specific enzymes to detoxify these defenses (see Chapter 3). On the one hand, production of detoxification enzymes (usually complex, energetically expensive molecules) reduces the net energy and nutritional value of food. On the other hand, these enzymes permit exploitation of a resource and derivation of nutritional value otherwise unavailable to the insect. Some insects not only detoxify host defenses but digest the products for use in their own metabolism and growth (e.g., Schöpf *et al*. 1982).

Many insects gain protected access to food (and habitat) resources through symbiotic interactions (i.e., living on or in food resources; see Chapter 8). Phytophagous species frequently spend most or all of their developmental period on host resources. A variety of myrmecophilous or termitophilous species are tolerated, or even share food with their hosts, as a result of morphological

TABLE 4.2 Components of the benefit-to-cost (B/C) ratio for individual *Paraponera clavata* and *Pogonomyrmex occidentalis* foragers.

	Paraponera		**Pogonomyrmex**
	Nectar Forager	**Prey Forager**	
Energy cost per m (J m^{-1})	0.042		0.007
Foraging trip distance (m)	125		12
Energy expenditure per trip (J)	5.3		0.09
Average reward per trip (J)	20.8	356	100
B/C	3.9	67	1111

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(size, shape and coloration), physiological (chemical communication), or behavioral (imitation of ant behavior, trophallaxis) adaptations (Wickler 1968). Resemblance to ants also may confer protection from other predators (see later in this chapter).

B. Mating Activity

Mate attraction and courtship behavior often are highly elaborated and ritualized and can be energetically costly. Nevertheless, such behaviors that distinguish species, especially sibling species, ensure appropriate mating and reproductive success and contribute to individual fitness through improved survival of offspring of sexual, as opposed to asexual, reproduction.

1. Attraction

Chemical, visual, and acoustic signaling are used to attract potential mates. Attraction of mates can be accomplished by either sex in Coleoptera, but only females of Lepidoptera release sex pheromones and only males of Orthoptera stridulate.

Sex pheromones greatly improve the efficiency with which insects find potential mates over long distances in heterogeneous environments (Cardé 1996, Law and Regnier 1971, Mustaparta 1984). The particular blend of compounds and their enantiomers, as well as the time of calling, varies considerably among species. These mechanisms represent the first step in maintaining reproductive isolation. For example, among tortricids in eastern North America, *Archips mortuanus* uses a 90:10 blend of (Z)-11- and (E)-11-tetradecenyl acetate, *A. argyrospilus* uses a 60:40 blend, and *A. cervasivoranus* uses a 30:70 blend. A related species, *Argyrotaenia velutinana* also uses a 90:10 blend but is repelled by (Z)-9-tetradecenyl acetate that is incorporated by *A. mortuanus* (Cardé and Baker 1984). Among three species of saturniids in South Carolina, *Callosamia promethea* is active from about 10:00–16:00, *C. securifera* from about 16:00–19:00, and *C. angulifera* from 19:00–24:00 (Cardé and Baker 1984). Bark beetle pheromones also have been studied extensively (e.g., Raffa *et al.* 1993). Representative bark beetle pheromones are shown in Fig. 4.2.

Sex pheromones may be released passively, as in the feces of bark beetles (Raffa *et al.* 1993), or actively through extrusion of scent glands and active "calling" (Cardé and Baker 1984). The attracted sex locates the signaler by following the concentration gradient (Fig. 4.3). Early studies suggested that the odor from a point source diffuses in a cone-shaped plume that expands downwind, the shape of the plume depending on airspeed and vegetation structure (e.g., Matthews and Matthews 1978). However, more recent work (Cardé 1996, Mafra-Neto and Cardé 1995, Murlis *et al.* 1992, Roelofs 1995) indicates that this plume is neither straight nor homogeneous over long distances but is influenced by turbulence in the airstream that forms pockets of higher concentration or absence of the vapor (Fig. 4.4). An insect downwind would detect the plume as odor bursts rather than as a constant stream. Heterogeneity in vapor concentration is augmented by pulsed emission by many insects.

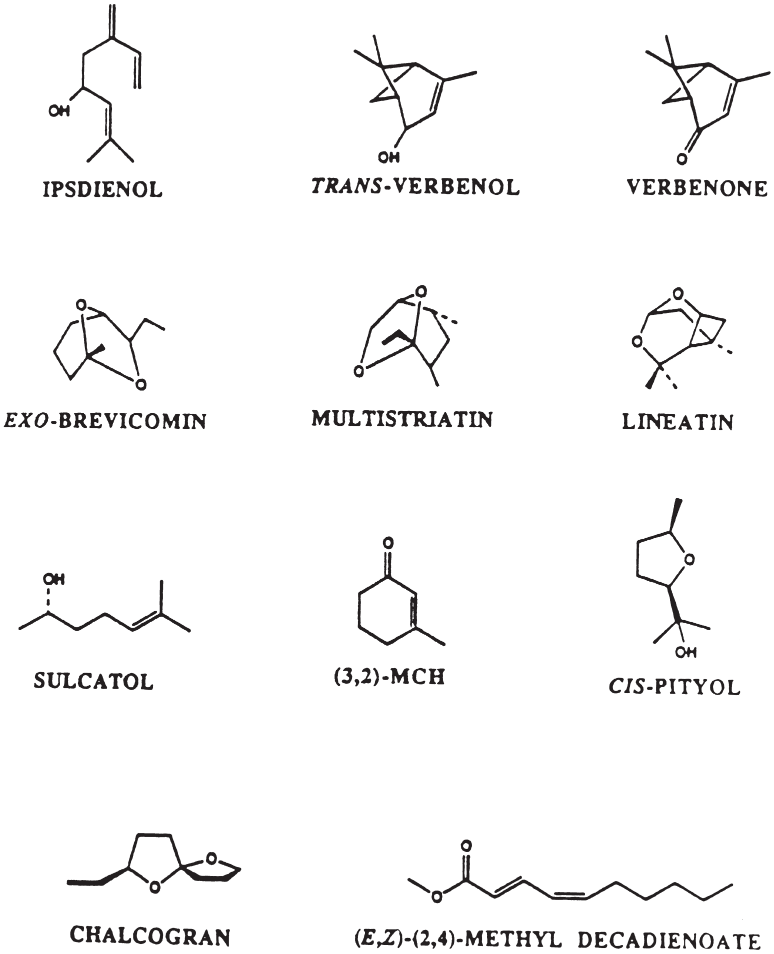


FIG. 4.2 Representative pheromones produced by bark beetles. Pheromones directly converted from plant compounds include ipsdienol (from myrcene), trans-verbenol, and verbenone (from α-pinene). The other pheromones shown are presumed to be synthesized by the beetles. From Raffa *et al.* (1993).

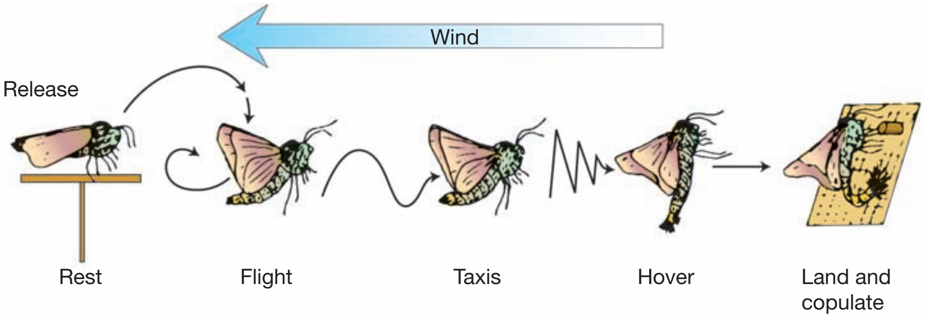


FIG. 4.3 Typical responses of male noctuid moths to the sex pheromone released by female moths. From Tumlinson and Teal (1987).

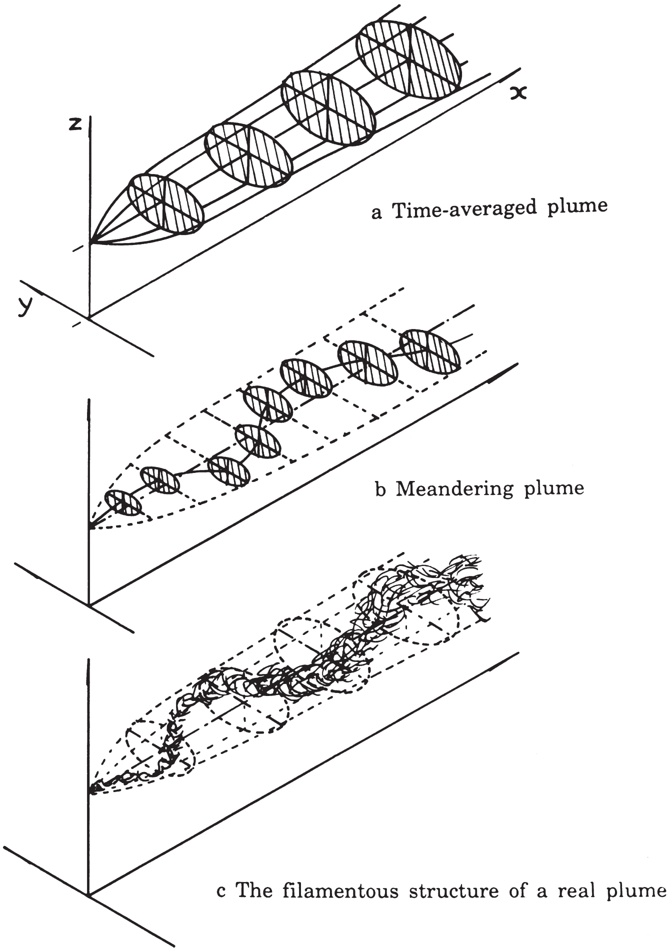


FIG. 4.4 Models of pheromone diffusion from a point source. The time-averaged Gaussian plume model (*a*) depicts symmetrical expansion of a plume from the point of emission. The meandering plume model (*b*) depicts concentration in each disc distributed normally around a meandering center line. The most recent work has demonstrated that pheromone plumes have a highly filamentous structure (*c*). From Murlis *et al.* (1992) with permission from the Annual Review of Entomology, Vol. 37, © 1992 by Annual Reviews.

Pulses in emission and reception may facilitate orientation because the antennal receptors require intermittent stimulation to avoid saturation and sustain upwind flight (Roelofs 1995). However, Cardé (1996) noted that the heterogeneous nature of the pheromone plume may make direct upwind orientation difficult over long distances. Pockets of little or no odor may cause the attracted insect to lose the odor trail. Detection can be inhibited further by openings in the vegetation canopy that create warmer convection zones or "chimneys" that carry the pheromone through the canopy (Fares *et al.* 1980). Attracted insects may increase their chances of finding the plume again by casting (i.e., sweeping back and forth in an arcing pattern until the plume is contacted again) (Cardé 1996). Given the small size of most insects and limited quantities of pheromones for release, mates must be able to respond to very low concentrations. Release of less than 1 ug sec^{-1} by female gypsy moth, *Lymantria dispar*, or silkworm, *Bombyx mori,* can attract males, which respond at molecular concentrations as low as 100 molecules ml^{-1} of air (Harborne 1994). Nevertheless, the likelihood of attracted insects reaching a mate is small. Elkinton *et al*. (1987) reported that the proportion of male gypsy moths responding to a caged female declined from 89% at 20 m distance to 65% at 120 m. Of those males that responded, the proportion arriving at the female's cage declined from 45% at 20 m to 8% at 120 m, and the average minimum time to reach the female increased from 1.7 min at 20 m to 8.9 min at 120 m (Fig. 4.5). Therefore, the probability of successful attraction of mates is low, and exposure to predators or other mortality factors is relatively high, over modest distances.

Visual signaling is exemplified by the fireflies (Coleoptera: Lampyridae) (e.g., Lloyd 1983). In this group of insects, different species distinguish each other by variation in the rhythm of flashing and by the perceived "shape" of flashes produced by distinctive movements while flashing. Other insects, including glowworms (Coleoptera: Phengodidae) and several midges, also attract mates by producing luminescent signals.

Acoustic signaling is produced by stridulation, particularly in the Orthoptera, Heteroptera, and Coleoptera, or by muscular vibration of a membrane, common in the Homoptera. Resulting sounds can be quite loud and detectable over con-

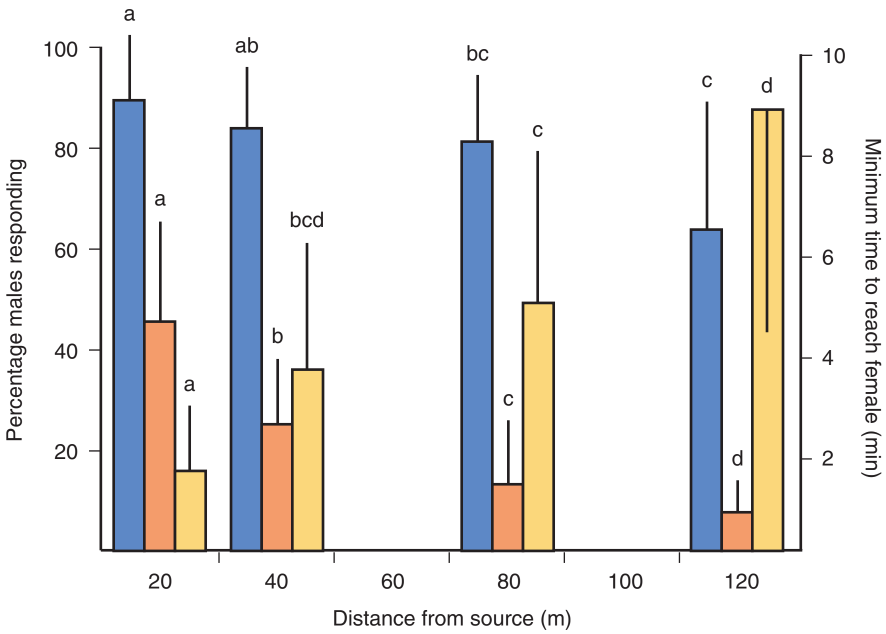


FIG. 4.5 Effect of distance on insect perception of and arrival at a pheromone source. Proportion (mean ± SD) of male gypsy moths responding at 20, 40, 80, and 120 m from a pheromone source (*black bar*), mean proportion of those responding that reached the source within a 40-min period (*gray bar*), and the average minimum time to reach the source (*white bar*); n = 23. Values followed by the same letter do not differ significantly at $P < 0.05$. Data from Elkinton *et al*. (1987).

siderable distances. For example, the acoustic signals of mole crickets, *Gryllotalpa vinae*, amplified by the double horn configuration of the cricket's burrow, are detectable by humans up to 600 m away (Matthews and Matthews 1978).

During stridulation, one body part, the file (consisting of a series of teeth or pegs), is rubbed over an opposing body part, the scraper. Generally, these structures occur on the wings and legs (R. Chapman 1982), but in some Hymenoptera sound also is produced by the friction between abdominal segments as the abdomen is extended and retracted. The frictional sound produced can be modulated by various types of resonating systems. Frequency and pattern of sound pulses are species specific.

Sound produced by vibrating membranes (tymbals) is accomplished by contracting the tymbal muscle to produce one sound pulse and relaxing the muscle to produce another sound pulse. Muscle contraction is so rapid (170–480 contractions per second) that the sound appears to be continuous (Matthews and Matthews 1978). The intensity of the sound is modified by air sacs operated like a bellows and by opening and closing opercula that cover the sound organs (R. Chapman 1982).

Such mechanisms greatly increase the probability of attracting mates. However, many predators also are attracted to, or imitate, signaling prey. For example, some firefly species imitate the flash pattern of prey species (Lloyd 1983).

2. Courtship Behavior

Courtship often involves an elaborate, highly ritualized sequence of stimulus and response actions that must be completed before copulation occurs (Fig. 4.6). This provides an important mechanism that identifies species and sex, thereby enhancing reproductive isolation. Color patterns, odors, and tactile stimuli are important aspects of courtship. For many species, ultraviolet patterns are revealed, close-range pheromones are emitted, or legs or mouthparts stroke the mate as necessary stimuli (L. Brower *et al*. 1965, Matthews and Matthews 1978).

Another important function of courtship displays in predatory insects is appeasement, or inhibition of predatory responses, especially of females. Nuptial feeding occurs in several insect groups, particularly the Mecoptera, empidid flies, and some Hymenoptera and Heteroptera (Fig. 4.7). The male provides a food gift (such as a prey item, nectar, seed, or glandular product) that serves at least two functions (Matthews and Matthews 1978, Price 1997, Thornhill 1976). Males with food may be more conspicuous to females, and feeding the female prior to oviposition may increase fecundity and fitness. Nuptial feeding has become ritualistic in some insects. Rather than prey, some flies simply offer a silk packet.

Conner *et al*. (2000) reported that male arctiid moths, *Cosmosoma myradora*, acquire pyrrolizidine alkaloids from excrescent fluids of some plants, such as *Eupatorium capillifolium.* The alkaloids are incorporated into cuticular filaments that are stored in abdominal pouches and discharged on the female during courtship. This topical application makes the female distasteful to spiders. Alkaloid-deprived males do not provide this protection, and females mated with such males are suitable prey for spiders.

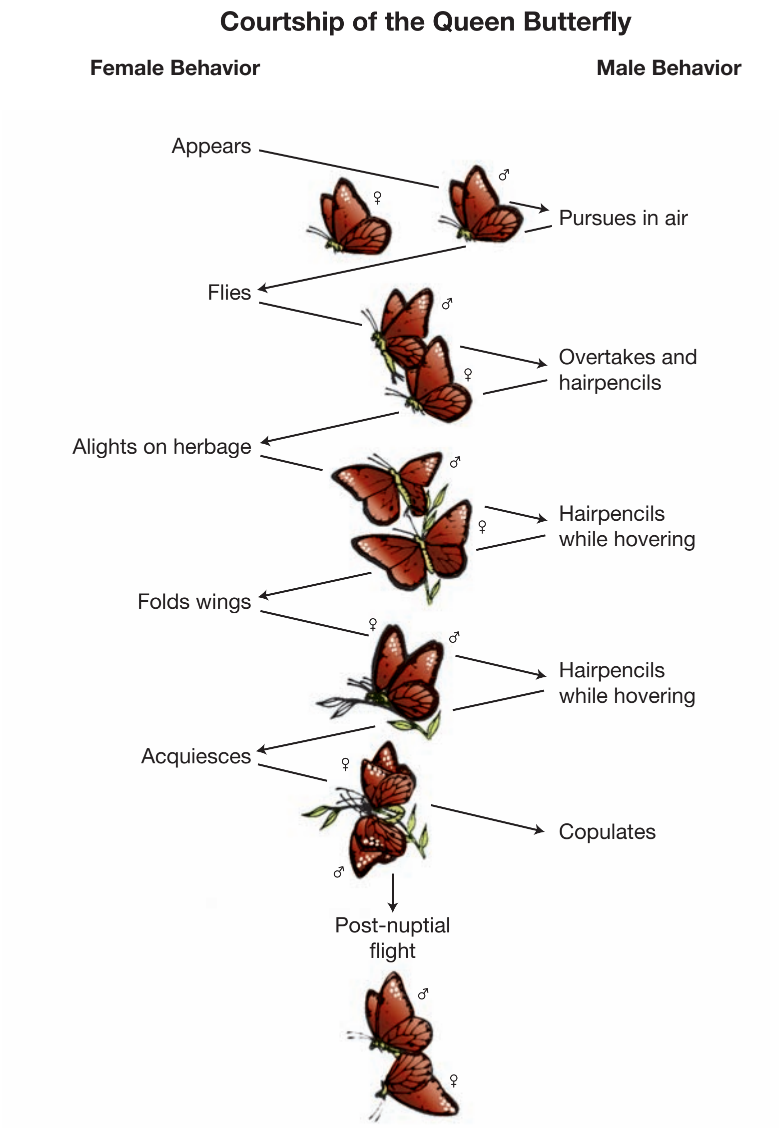


FIG. 4.6 Courtship stimulus-response sequence of the Queen butterfly from top to bottom, with male behavior on the right and female behavior on the left. From L. Brower *et al*. (1965) with permission of the Wildlife Conservation Society.

Males of some flies, euglossine bees, Asian fireflies, and some dragonflies gather in groups, called leks, to attract and court females (Fig. 4.7). Such aggregations allow females to compare and choose among potential mates and facilitate mate selection.

C. Reproductive and Social Behavior

Insects, like other organisms, invest much of their assimilated energy and nutrient resources in the production of offspring. Reproductive behavior includes

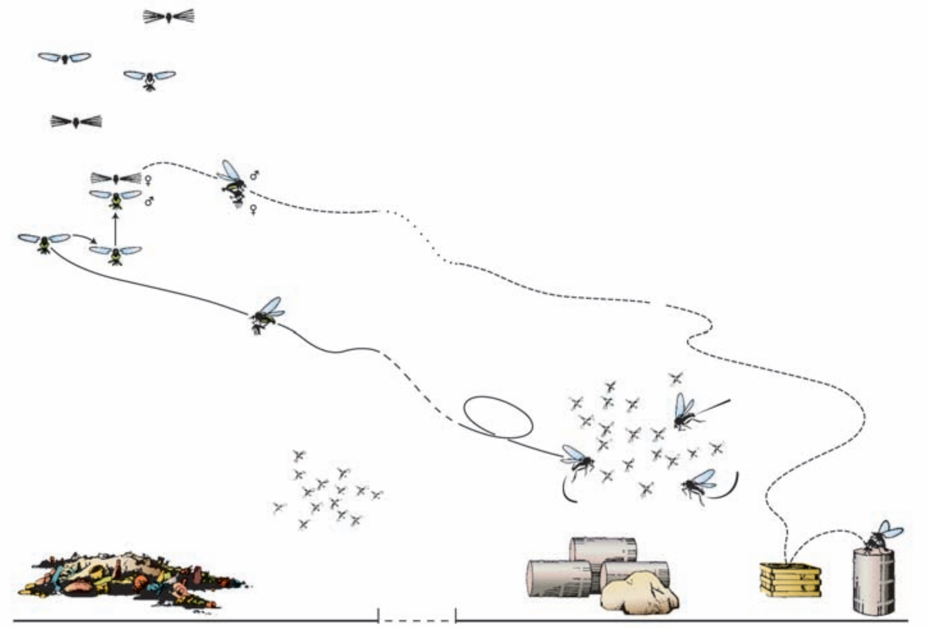


FIG. 4.7 Example of lekking and appeasement behavior in the courtship of an empidid fly, *Rhamphomyia nigripes.* Males capture a small insect, such as a mosquito and midge, then fly to a mating swarm (lek), which attracts females. Females select their mates and obtain the food offering. The pair then leaves the swarm and completes copulation on nearby vegetation. From Downes (1970) with permission from the Entomological Society of Canada.

varying degrees of parental investment in offspring that determines the survival of eggs and juveniles. Selection of suitable sites for oviposition affects the exposure of eggs to abiotic conditions suitable for hatching. The choice of oviposition site also affects the exposure of hatching immatures to predators and parasites and their proximity to suitable food resources. Nesting behavior, brood care, and sociality represent stages in a gradient of parental investment in survival of offspring.

1. Oviposition Behavior

Insects deposit their eggs in a variety of ways. Most commonly, the female is solely responsible for selection of oviposition site(s). The behaviors leading to oviposition are as complex as those leading to mating because successful oviposition contributes to individual fitness and is under strong selective pressure.

A diversity of stimuli affects choice of oviposition sites by female insects. Mosquitoes are attracted to water by the presence of vegetation and reflected light, but they lay eggs only if salt content, pH, or other factors sensed through tarsal sensillae are suitable (Matthews and Matthews 1978). Grasshoppers assess the texture, salinity, and moisture of soil selected for oviposition.

Many phytophagous insects assess host suitability for development of offspring. This assessment may be on the basis of host chemistry or existing feeding pressure. Ovipositing insects tend to avoid host materials with deleterious levels of secondary chemicals. They also may avoid ovipositing on resources that are already occupied by eggs or competitors. For example, female bean weevils, *Callosobruchus maculatus*, assess each potential host bean by comparison to the previous bean and lay an egg only if the present bean is larger or has fewer eggs. The resulting pattern of oviposition nearly doubles larval survival compared to random oviposition (R. Mitchell 1975). Many parasitic wasps mark hosts in which eggs have been deposited and avoid ovipositing in marked hosts, thereby minimizing larval competition within a host (Godfray 1994). Parasitic wasps can minimize hyperparasitism by not ovipositing in more than one host in an aggregation. This reduces the risk that all of its offspring are found and parasitized (Bell 1990). Cannibalistic species, such as *Heliconius* butterflies, may avoid laying eggs near each other to minimize cannibalism and predation.

Selection also determines whether insects lay all their eggs during one period (semelparity) or produce eggs over more protracted periods (iteroparity). Most insects with short life cycles (e.g., <1 year) usually have relatively short adult life spans and lay all their eggs in a relatively brief period. Insects with longer life spans, especially social insects, reproduce continually for many years.

Some insects influence host suitability for their offspring. For example, female sawflies usually sever the resin ducts at the base of a conifer needle prior to laying eggs in slits cut distally to the severed ducts. This behavior prevents or reduces egg mortality resulting from resin flow into the oviposition slits (McCullough and Wagner 1993). Parasitic Hymenoptera often inject mutualistic viruses into the host along with their eggs. The virus inhibits cellular encapsulation of the egg or larva by the host (Tanada and Kaya 1993).

In other cases, choices of oviposition sites by adults clearly conflict with suitability of resources for offspring. Kogan (1975) and Courtney (1985, 1986) reported that some species preferentially oviposit on the most conspicuous (apparent) host species that are relatively unsuitable for larval development (see Fig. 3.10). However, this behavior represents a tradeoff between the prohibitive search time required to find the most suitable hosts and the reduced larval survival on the more easily discovered hosts.

2. *Nesting and Brood Care*

Although brood care is best known among the social insects, other insects exhibit maternal care of offspring and even maternal tailoring of habitat conditions to enhance survival of offspring. Primitive social behavior appears as parental involvement extends further through the development of their offspring.

Several environmental factors are necessary for evolution of parental care (E. Wilson 1975). A stable environment favors larger, longer-lived species that reproduce at intervals, rather than all at once. Establishment in new, physically stressful environments may select for protection of offspring, at least during vulnerable periods. Intense predation may favor species that guard their young to improve their chances of reaching breeding age. Finally, selection may favor species that invest in their young, which, in turn, help the parent find, exploit, or guard food resources. Cooperative brood care, involving reciprocal communication, among many adults is the basis of social organization (E. Wilson 1975).

A variety of insect species from several orders exhibit protection of eggs by a parent (Matthews and Matthews 1978). In most cases, the female remains near her eggs and guards them against predators. However, in some species of giant water bugs (*Belostoma* and *Abedus*), the eggs are laid on the back of the male, which carries them until they hatch. Among dung beetles (Scarabaeidae), adults of some species limit their investment in offspring to providing protected dung balls in which eggs are laid, whereas females in the genus *Copris* remain with the young until they reach adulthood.

Extended maternal care, including provision of food for offspring, is seen in crickets, cockroaches, some Homoptera, and nonsocial Hymenoptera. For example, females of the membracid, *Umbonia crassicornis,* enhance offspring survival by brooding eggs, cutting slits in the bark of twigs to facilitate feeding by nymphs, and defending nymphs against predators (T. Wood 1976). Survival of nymphs with their mother present was 80%, compared to 60% when the mother was removed 2–3 days after egg hatch and 10% when the mother was removed prior to making bark slits. Females responded to predators or to alarm pheromones from injured offspring by fanning wings and buzzing, usually driving the predator away (T. Wood 1976).

A number of arthropod species are characterized by aggregations of individuals. Groups can benefit their members in a number of ways. Large groups often are able to modify environmental conditions, such as through retention of body heat or moisture. Aggregations also increase the availability of potential mates (Matthews and Matthews 1978) and minimize exposure of individuals to plant toxins (McCullough and Wagner 1993, Nebeker *et al*. 1993) and to predators (Fitzgerald 1995). Aggregated, cooperative feeding on plants, such as by sawflies and bark beetles, can remove plant tissues or kill the plant before induced defenses become effective (McCullough and Wagner 1993, Nebeker *et al*. 1993). Groups limit predator ability to avoid detection and to separate an individual to attack from within a fluid group. Predators are more vulnerable to injury by surrounding individuals, compared to attacking isolated individuals.

Cooperative behavior is evident within groups of some spiders and communal herbivores, such as tent-building caterpillars and gregarious sawflies. Dozens of individuals of the spider *Mallos gragalis* cooperate in construction of a communal web and in subduing prey (Matthews and Matthews 1978). Tent-building caterpillars cooperatively construct their web, which affords protection from predators and may facilitate feeding and retention of heat and moisture (Fitzgerald 1995). Similarly, gregarious sawflies cooperatively defend against predators and distribute plant resin among many individuals, thereby limiting the effectiveness of the resin defense (McCullough and Wagner 1993).

Primitive social behavior is exhibited by the woodroach, *Cryptocercus punctulatus;* by passalid beetles; and by many Hymenoptera. In these species, the young remain with the parents in a family nest for long periods, are fed by the parents, and assist in nest maintenance (Matthews and Matthews 1978). However, these insects do not exhibit coordinated behavior or division of labor among distinct castes.

The complex eusociality characterizing termites and the social Hymenoptera has attracted considerable attention (e.g., Matthews and Matthews 1978, E.

Wilson 1975). Eusociality is characterized by multiple adult generations and highly integrated cooperative behavior, with efficient division of labor, among all castes (Matthews and Matthews 1978, Michener 1969). Members of these insect societies cooperate in food location and acquisition, feeding of immatures, and defense of the nest. This cooperation is maintained through complex pheromonal communication, including trail and alarm pheromones (Hölldobler 1995, see Chapter 3), and reciprocal exchange of regurgitated liquid foods (trophallaxis) between colony members. Trophallaxis facilitates recognition of nest mates by maintaining a colony-specific odor, ensures exchange of important nutritional resources and (in the case of termites) of microbial symbionts that digest cellulose, and may be critical to colony survival during periods of food limitation (Matthews and Matthews 1978). Trophallaxis distributes material rapidly throughout a colony (M. Suarez and Thorne 2000). E. Wilson and Eisner (1957) fed honey mixed with radioactive iodide to a single worker ant and within 1 day detected some tracer in every colony member, including the two queens. Such behavior may also facilitate spread of pathogens or toxins throughout the colony (J. K. Grace and Su 2000, Shelton and Grace 2003).

Development of altruistic behaviors such as social cooperation can be explained largely as a consequence of kin selection and reciprocal cooperation (Axelrod and Hamilton 1981, Haldane 1932, Hamilton 1964, Trivers 1971, E. Wilson 1973, Wynne-Edwards 1963, 1965, see also Chapter 15). Self-sacrifice that increases reproduction by closely related individuals increases inclusive fitness (i.e., the individual's own fitness plus the fitness accruing to the individual through its contribution to reproduction of relatives). In the case of the eusocial Hymenoptera, because of haploid males, relatedness among siblings is greater than that between parent and offspring, making cooperation among colony members highly adaptive. The epitome of "altruism" among insects may be the development of the barbed sting in the worker honey bee, *Apis mellifera*, that ensures its death in defense of the colony (Haldane 1932, Hamilton 1964). Termites do not share the Hymenopteran model for sibling relatedness. Genetic data for termites indicate relatively high inbreeding and relatedness within colonies and kin-biased foraging behavior for some species (Kaib *et al*. 1996, Vargo *et al*. 2003). However, Husseneder *et al*. (1999) reported that DNA (deoxyribonucleic acid) analysis of colonies of the African termite, *Schedorhinotermes lamanianus,* did not indicate effective kin selection through inbreeding or translocation complexes of sex-linked chromosomes that could generate higher relatedness within than between sexes. They concluded that ecological factors, such as predation and food availability, may be more important than genetics in maintaining termite eusociality, at least in this species.

D. Competitive, Defensive, and Mutualistic Behavior

Insects, like all animals, interact with other species in a variety of ways, as competitors, predators, prey, and mutualists. Interactions among species will be discussed in greater detail in Chapter 8. These interactions require varying degrees of energy or nutrient expenditure, or both. Contests among individuals for resources occasionally involve combat. Subduing prey and defending against predators also involve strenuous activity. Mutualism requires reciprocal exchange of resources or services. Obviously, these activities affect the energy and nutrient budgets of individual organisms.

1. Competitive Behavior

Competition occurs among individuals using the same limiting resources at the same site. Energy expended, or injury suffered, defending resources or searching for uncontested resources affects fitness. Competition often is mediated by mechanisms that determine a dominance hierarchy. Establishment of dominant and subordinate status among individuals limits the need for physical combat to determine access to resources and ensures that dominant individuals get more resources than do subordinate individuals.

Visual determination of dominance status is relatively rare among insects, largely because of their small size; the complexity of the environment, which restricts visual range; and the limitations of fixed-focus compound eyes for long-distance vision (Matthews and Matthews 1978). Dragonflies have well-developed eyes and exhibit ritualized aggressive displays that maintain spacing among individuals. For example, male *Plathemis lydia* have abdomens that are bright silvery-white above. Intrusion of a male into another male's territory initiates a sequence of pursuit and retreat, covering a distance of 8–16 m. The two dragonflies alternate roles and directions, with the abdomens raised during pursuit and lowered during retreat, until the intruder moves to another site (P. Corbet 1962).

Mediation of competition by pheromones has been documented for several groups of insects. Adult flour beetles, *Tribolium*, switch from aggregated distribution at low densities to random distribution at intermediate densities, to uniform distribution at high densities. This spacing is mediated by secretion of quinones, repellent above a certain concentration, from thoracic and abdominal glands (Matthews and Matthews 1978). Larvae of the flour moth, *Anagasta kunniella*, secrete compounds, from the mandibular glands, that increase dispersal propensity, lengthen generation time, and reduce the fecundity of females that were crowded as larvae (Matthews and Matthews 1978). Bark beetles use repellent pheromones, as well as acoustic signals, to maintain minimum distances between individuals boring through the bark of colonized trees (Raffa *et al*. 1993, Rudinsky and Ryker 1976). Ant colonies also maintain spacing through marking of foraging trails with chemical signals (see earlier in this chapter and Chapter 3).

Acoustic signals are used by many Orthoptera and some Coleoptera to deter competitors. Bark beetles stridulate to deter other colonizing beetles from the vicinity of their gallery entrances (Rudinsky and Ryker 1976). Subsequently, excavating adults and larvae respond to the sounds of approaching excavators by mining in a different direction, thus preventing intersection of galleries. Some male crickets and grasshoppers produce a distinctive rivalry song when approaching each other (Matthews and Matthews 1978, Schowalter and Whitford 1979). The winner (continued occupant) usually is the male that produces more of this aggressive stridulation.

When resources are relatively patchy, males may increase their access to females by marking and defending territories that contain resources attractive to females. Territorial behavior is less adaptive (i.e., costs of defending resources exceeds benefits) when resources are highly concentrated and competition is severe or when resources are uniformly distributed and female distribution is less predictable (Baker 1972, Schowalter and Whitford 1979).

Marking territorial boundaries takes a variety of forms among animal taxa. Male birds mark territories by calling from perches along the perimeter. Male deer rub scent glands and scrape trees with their antlers to advertise their territory. Social insects, including ants, bees, and termites, mark nest sites and foraging areas with trail pheromones that advertise their presence. These trail markers can be perceived by other insects at minute concentrations (see Chapter 3). Many orthopterans and some beetles advertise their territories by stridulating.

However, many insects advertise their presence simply to maintain spacing and do not actively defend territories. Similarly, males of many species, including insects, fight over receptive females. E. Wilson (1975) considered defense of occupied areas to be the defining criterion for territoriality. Territorial defense is best known among vertebrates, but a variety of insects representing at least eight orders defend territories against competitors (Matthews and Matthews 1978, Price 1997). Because territorial defense represents an energetic cost, an animal must gain more of the resource by defending it against competitors than by searching for new resources. Nonaggressive males often "cheat" by nonadvertisement and quiet interception of resources or of females attracted to the territory of the advertising male (Schowalter and Whitford 1979).

The type of territory differs among insect taxa, but usually it is associated with competition for food or mates (Matthews and Matthews 1978, Price 1997). Male crickets defend the area around their dens and mate with females attracted to their stridulation. Male eastern woodroaches, *Cryptocercus punctulatus*, defend mating chambers in rotten wood (Ritter 1964). Some insects that form leks defend small territories within the lek. Presumably, more females are attracted to this concentration of males, increasing mating success, than to isolated males (Price 1997). Such mating territories apparently are not related to food or oviposition sites but may maximize attraction of females.

Two grasshopper species, *Ligurotettix coquilletti* and *Bootettix argentatus*, that feed on creosote bush, *Larrea tridentata*, in the deserts of the southwestern United States are perhaps the only territorial acridoids (Otte and Joern 1975, Schowalter and Whitford 1979). These grasshoppers defend individual creosote bushes. The larger bushes are more likely to harbor females, and opportunities for mating are increased by defending larger shrubs, especially at low grasshopper population densities. Schowalter and Whitford (1979) reported that male movement from small shrubs was greater than movement from larger shrubs, and contests for larger shrubs occurred more frequently. However, fewer males defended territories at high population densities, apparently because interception of females by nonstridulating males and more frequent combat decreased mating success of territorial defenders.

Males of the speckled wood butterfly, *Pararge aegeria* (Satyridae), defend sunspots on the forest floor, apparently because females are attracted to resources that occur in sunspots (Price 1997). Only 60% of the males held such territories, but these encountered many more females than did the nonterritorial males that searched for mates in the forest canopy. Defense of an oviposition site may be advantageous where sperm competition cannot be avoided by anatomical or physiological means, such as with mating plugs that prevent subsequent mating. Another butterfly, *Inachis io*, defends territories at the approach to oviposition sites, perhaps because of selective pressure from strong competition at the oviposition sites (Baker 1972). Other insects, especially the social Hymenoptera, defend nests, foraging trails, or food (Price 1997).

The benefits of defending food resources or mates must be weighed against the costs of fighting, in terms of time, energy, and risk of injury. Territorial insects may abandon territorial defense at high population densities when time spent fighting detracts from feeding or mating success (Schowalter and Whitford 1979).

2. Defensive Behavior

Most insects are capable of defending themselves against predators. Mandibulate species frequently bite, and haustelate species may stab with their stylets. Kicking, wing fanning, and buzzing also are effective against some predators (Robinson 1969, T. Wood 1976). Many species eject or inject toxic or urticating chemicals, as described in Chapter 3 (see Figs. 3.7 and 3.8). Insects armed with urticating spines or setae often increase the effectiveness of this defense by thrashing body movements that increase contact of the spines or setae with an attacker. Many caterpillars and sawfly larvae rear up and strike like a snake when attacked (Fig. 4.8).

Insects produce a variety of defensive compounds that can deter or injure predators, as described in Chapter 3. Many of these compounds are energetically expensive to produce and may be toxic to the producer as well as to predators, requiring special mechanisms for storage or delivery. Nevertheless, their production sufficiently improves the probability of survival and reproduction to represent a net benefit to the producer (Conner *et al.* 2000, Sillén-Tullberg 1985). Such species usually are conspicuously colored (aposematic) to facilitate avoidance learning by predators (Fig. 4.9).

Defense conferred by camouflage reduces the energy costs of active defense but may require greater efficiency in foraging or other activities that could attract attention of predators (Schultz 1983). Insects that rely on resemblance to their background (crypsis) must minimize movement to avoid detection (Fig. 4.10). For example, many Homoptera that are cryptically colored or that resemble thorns or debris are largely sedentary while siphoning plant fluids. Many aquatic insects resemble benthic debris and remain motionless as they filter suspended matter. Cryptic species usually restrict necessary movement to nighttime or acquire their food with minimal movement, especially in the presence of predators (Johansson 1993). Such insects may escape predators by waiting until a predator is very close before flushing with a startle display, giving the predator insufficient warning to react. However, some birds use tail fanning or other scare

FIG. 4.8 Defensive posture of black swallowtail, *Papilio polyxenes*, caterpillar. This snake-like posture, together with emission of noxious volatiles from the orange protuberances, deters many would-be predators.

FIG. 4.9 Aposematic coloration. Seed bugs (Lygaeidae) often sequester toxins from their host plants and advertise their distasteful or toxic condition (Puerto Rico).

FIG. 4.10 Examples of cryptic coloration. Creosote bush grasshopper, *Bootettix argentatus*, in creosote bush, *Larrea tridentata* (New Mexico, United States) (*top*); moth with leaf-mimicking coloration and form (Taiwan) (*bottom*).

tactics to flush prey from a greater distance and thereby capture prey more efficiently (Galatowitsch and Mumme 2004, Jabłoński 1999, Mumme 2002).

Disruptive and deceptive coloration involve color patterns that break up the body form, distract predators from vital body parts, or resemble other predators. For example, many insects have distinct bars of color or other patterns that disrupt the outline of the body and inhibit their identification as prey by passing predators. Startle displays enhance the effect of color patterns (Robinson 1969). The underwing moths (Noctuidae) are noted for their brightly colored hind wings that are hidden at rest by the cryptically colored front wings. When threatened, the moth suddenly exposes the hind wings and has an opportunity to escape its startled attacker. The giant silkworm moths (Saturniidae) and eyed elater, *Alaus oculatus* (Coleoptera: Elateridae), have conspicuous eyespots that make these insects look like birds (especially owls) or reptiles. The eyespots of moths usually are hidden on the hind wings during rest and can be exposed suddenly to startle would-be predators. The margin of the front wings in some saturniids are shaped and colored to resemble the heads of snakes (Fig. 4.11) (Grant

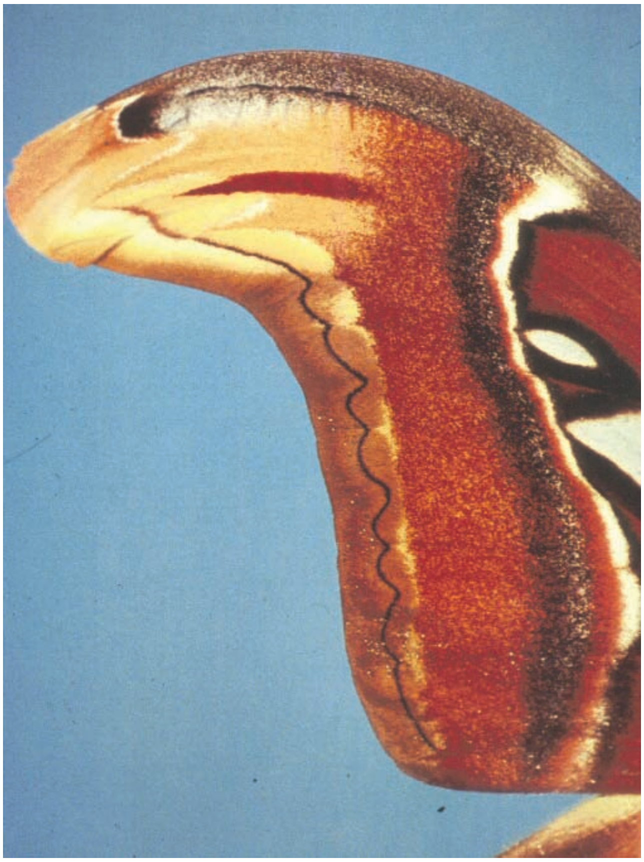


FIG. 4.11 Image of a snake's head on the wing margins of *Attacus atlas.* From Grant and Miller (1995) with permission from the Entomological Society of America.

and Miller 1995). Sudden wing movement during escape may enhance the appearance of a striking snake.

Mimicry is resemblance to another, usually venomous or unpalatable, species and usually involves conspicuous, or aposematic, coloration. Mimicry can take two forms, *Batesian* and *Müllerian.* Batesian mimicry is resemblance of a palatable or innocuous species to a threatening species, whereas Müllerian mimicry is resemblance among threatening species. Both are exemplified by insects. A variety of insects (representing several orders) and other arthropods (especially spiders) benefit from resemblance to stinging Hymenoptera. For example, clearwing moths (Sessidae) and some sphingid moths, several cerambycid beetles, and many asilid and syrphid flies resemble bees or wasps (Fig. 4.12). A variety of insect and other species gain protection through adaptations that permit them to mimic ants (Blum 1980, 1981). Müllerian mimicry is exemplified by sympatric species of Hymenoptera and heliconiid butterflies that sting, or are unpalatable, and resemble each other (e.g., A. Brower 1996, Sheppard *et al*. 1985).

Mimicry systems can be complex, including a number of palatable and unpalatable species and variation in palatability among populations, depending on food source. For example, the resemblance of the viceroy, *Limenitis archippus* (Nymphalidae), butterfly to the monarch, *Danaus plexippus* (Daneidae), butter-

FIG. 4.12 Batsian mimicry by two insects. The predaceous asilid fly on the left and its prey, a cerambycid beetle, both display the black and yellow coloration typical of stinging Hymenoptera.

fly generally is considered to be an example of Batesian mimicry. However, monarch butterflies show a spectrum of palatability over their geographic range, depending on the quality of their milkweed, and other, hosts (L. Brower *et al.* 1968). Furthermore, populations of the viceroy and monarch in Florida are equally distasteful (Ritland and Brower 1991). Therefore, this mimicry system may be Batesian in some locations and Müllerian in others. Conspicuous color patterns and widespread movement of the co-models/mimics maximizes exposure to predators and reinforces predator avoidance, providing overall protection against predation.

Sillén-Tullberg (1985) compared predation by great tits, *Parus major*, between normal aposematic (red) and mutant cryptic (grey) nymphs of the seed bug, *Lygaeus equestris.* Both prey forms were equally distasteful. All prey were presented against a grey background. Survival of aposematic nymphs was 6.4-fold higher than for cryptic nymphs because the birds showed a greater initial reluctance to attack, learned avoidance more rapidly, and killed prey less frequently during an attack. The greater individual survival of aposematic nymphs indicated sufficient benefit to explain the evolution of aposematic coloration.

Some insects alert other members of the population to the presence of predators. Alarm pheromones are widespread among insects. These compounds usually are relatively simple hydrocarbons, but more complex terpenoids occur among ants. The venom glands of stinging Hymenoptera frequently include alarm pheromones. Alarm pheromones function either to scatter members of a group when threatened by a predator, or to concentrate attack on the predator, especially among the social insects. A diverse group of ground-dwelling arthropods produce compounds that mimic ant alarm pheromones. These function to scatter attacking ants, allowing the producer to escape (Blum 1980). Alarm pheromones released with the venom are used by stinging Hymenoptera to mark a predator. This marker serves to attract, and concentrate attack by, other members of the colony.

3. *Mutualistic Behavior*

Insects participate in a variety of mutualistic interactions, including the well-known pollinator–plant, ant–plant, and wood borer–microorganism associations (see Chapter 8). Usually, mutualism involves diversion of resources by one partner to production of rewards or inducements that maintain mutualistic interactions. Various pollinators and predators exploit resources allocated by plants to production of nectar, domatia, root exudates, etc., and thereby contribute substantially to plant fitness. At the same time, the plant limits the nectar reward in each flower to force pollinators to transport pollen among flowers. During dispersal, bark beetles secrete lipids into mycangia to nourish mutualistic microorganisms that subsequently colonize wood and improve the nutritional suitability of woody substrates for the beetles. Obviously, the benefit gained from this association must outweigh these energetic and nutritional costs (see Chapter 8). Resources directed to support of mutualists could be allocated to growth and reproduction. These resources may be redirected if the partner is not present (e.g., Rickson 1977), although some species maintain such allocation for long periods in the absence of partners (Janzen and Martin 1982).

III. EFFICIENCY OF RESOURCE USE

Fitness accrues to organisms to the extent that they survive and produce more offspring than do their competitors. Hence, the efficiency with which assimilated resources are allocated to growth and reproduction determines fitness. However, except for sessile organisms, much of the assimilated energy and material must be allocated to activities pursuant to food acquisition, dispersal, mating, competition, and defense. The amount of assimilated resources allocated to these activities reduces relative growth efficiency (Schultz 1983, Zera and Denno 1997). Clearly, the diversion of resources from growth and reproduction to these other pathways must represent a net benefit to the insect.

A. Factors Affecting Efficiency

Efficiency is affected by a number of constraints on energy and resource allocation. Clearly, selection should favor physiological and behavioral adaptations that improve overall efficiency. However, adaptive strategies reflect the net current result of many factors that have variable and interactive effects on survival and reproduction. Hence, individual responses to current conditions vary in efficiency. Whereas physiological, and many behavioral, responses are innate (genetically based, hence relatively inflexible), the capacity to learn can improve efficiency greatly, by reducing the time and resources expended in responding to environmental variation (Cunningham *et al*. 1998, A. Lewis 1986).

Hairston *et al*. (1960) stimulated research on the constraints of food quality on efficiency of herbivore use of resources by postulating that all plant material is equally suitable for herbivores. Just as plant chemical defenses can reduce herbivore efficiency, various animal defenses increase the resource expenditure necessary for predators to capture and assimilate prey. In addition to factors affecting the efficiency of resource acquisition, several factors affect the efficiency of resource allocation, including food quality, size, physiological condition, and learning.

1. *Food Quality*

Food quality affects the amount of food required to obtain sufficient nutrition for growth and reproduction, and the energy and nutrients required for detoxification and digestion (see Chapter 3). Insects feeding on hosts with lower levels of defensive compounds invest fewer energy and nutrient resources in detoxification enzymes or continued searching behavior than do insects feeding on better defended hosts. Herbivores process much indigestible plant material, especially cellulose, whereas predators process animal material that generally is more similar to their own tissues. Accordingly, we might expect higher assimilation efficiencies for predators than for herbivores (G. Turner 1970). Although indigestible and toxic compounds in plant tissues reduce assimilation efficiency for herbivores (Scriber and Slansky 1981), toxins sequestered or produced by prey also reduce assimilation efficiency of predators. However, few studies have addressed the effect of toxic prey on assimilation efficiency of predators (L. Dyer 1995, Stamp *et al.* 1997, Stephens and Krebs 1986).

Insects may ingest relatively more food to obtain sufficient nutrients or energy to offset the costs of detoxification or avoidance of plant defensive chemicals. Among herbivores, species that feed on mature tree leaves have relative growth rates that are generally half the values for species that feed on forbs because tree leaves are poor food resources compared to forbs (Scriber and Slansky 1981). Although specialists might be expected to feed more efficiently on their hosts than do generalists, Futuyma and Wasserman (1980) reported that a specialist (the eastern tent caterpillar, *Malacosoma americana*) had no greater assimilation or growth efficiencies than did a generalist (the forest tent caterpillar, *M. disstria*). Some wood-boring insects may require long periods (several years to decades) of larval feeding to concentrate nutrients (especially N and P) sufficient to complete development.

2. Size and Physiological Condition

Body size is a major factor affecting efficiency of energy use. Larger organisms have greater energy requirements than do smaller organisms. However, smaller organisms with larger surface area-to-volume ratios are more vulnerable to heat loss than are larger organisms. Accordingly, maintenance energy expenditure per unit body mass decreases with increasing body size (Phillipson 1981). In addition, larger organisms tend to use energy more efficiently during movement and resource acquisition, have a competitive advantage in cases of direct aggression, and have greater immunity from predators (Ernsting and van der Werf 1988, Heinrich 1979, Phillipson 1981, Streams 1994), reducing relative energy expenditures for these activities.

Physiological condition, including the general vigor of the insect as affected by parasites, also influences food requirements and assimilation efficiency. For example, hunger may induce increased effort to gain resources that would be ignored by less desperate individuals (Ernsting and van der Werf 1988, Holling 1965, Iwasaki 1990, 1991, Richter 1990, Streams 1994). Slansky (1978) reported that cabbage white butterfly larvae parasitized by *Apanteles glomeratus* (Hymenoptera) increased food consumption, growth rate, and nitrogen assimilation efficiency. Schowalter and Crossley (1982) found that Madagascar hissing cockroaches, *Gromphadorhina portentosa*, with associated mites, *Gromphadorholaelaps schaeferi*, had a significantly greater egestion rate than did cockroaches with mites excluded, although assimilation efficiency did not differ significantly between mite-infested and mite-free cockroaches (Fig. 4.13).

3. Learning

Learning is a powerful tool for improving efficiency of resource use (see Chapter 3). Learning reduces the effort wasted in unsuccessful trials (see Fig. 3.15). Learning to distinguish appropriate from inappropriate prey (e.g., search image), to respond to cues associated with earlier success, and to improve foraging tech-

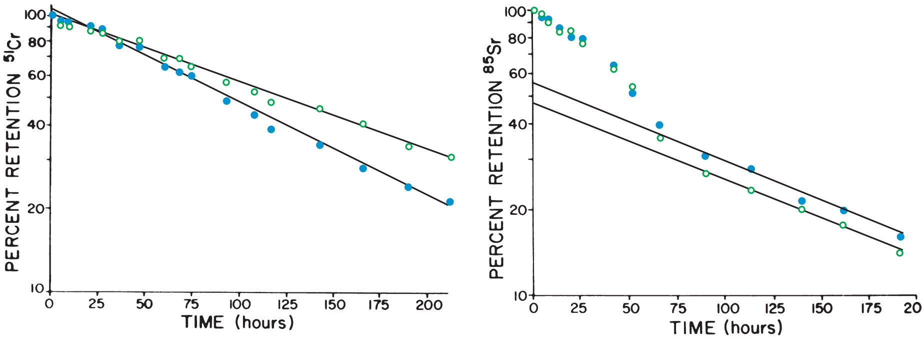


FIG. 4.13 Bioelimination of ^{51}Cr (*left*) and ^{85}Sr (*right*) by the cockroach, *Gromphadorhina portentosa* with (*solid blue circles*) and without (*open green circles*) the associated mite, *Gromphadorholaelaps schaeferi.* ^{51}Cr has no biological function and its elimination represents egestion; ^{85}Sr is an analog of Ca and its elimination represents both egestion (regression lines similar to those for ^{51}Cr) and excretion of assimilated isotope (rapid initial loss). This insect appears to assimilate and begin excreting nutrients before gut passage of unassimilated nutrients is complete. From Schowalter and Crossley (1982) with permission from the Entomological Society of America.

nique greatly facilitates energy and nutrient acquisition (Cunningham *et al.* 1998). Honey bees represent the epitome of resource utilization efficiency among insects through their ability to communicate foraging success and location of nectar resources to nestmates (F. Dyer 2002, J. Gould and Towne 1988, Heinrich 1979, von Frisch 1967).

B. Tradeoffs

Allocation efficiency often is optimized by adaptations that generally tailor insect morphology, life histories, or behavior to prevailing environmental conditions or resource availability. For example, synchronization of life histories with periods of suitable climatic conditions and food availability reduces the energy required for thermoregulation or search activity. Bumble bee, *Bombus* spp., anatomy optimizes heat retention during foraging in cool temperate and arctic habitats (Heinrich 1979). Davison (1987) compared the energetics of two harvester ant species, *Chelaner rothsteini* and *C. whitei*, in Australia and found that the smaller *C. rothsteini* had lower assimilation efficiency but higher production efficiency (largely in production of offspring) than did the larger *C. whitei. Chelaner rothsteini* discontinued activity during the winter, perhaps to avoid excessive metabolic heat loss, whereas *C. whitei* remained active all year.

Selection should favor individuals and species that acquire and allocate resources most efficiently. Males that defend territories when the time or energy spent on this activity interferes with mating and reproduction are less likely to contribute to the genetic composition of the next generation than are males that sacrifice territorial defense for mating opportunities under such conditions (Schowalter and Whitford 1979).

However, as discussed earlier in this chapter, female pierid butterflies oviposited preferentially on more conspicuous hosts, a more energetically efficient search strategy for the adult, but these hosts were less suitable for larval development than were less conspicuous hosts (see Fig. 3.10) (Courtney 1985, 1986). Similarly, females of the noctuid moth, *Autographa precationis*, preferentially oviposit on soybeans, rather than on dandelions, perhaps because the shape of dandelions is a less effective oviposition stimulus, although larvae show a marked feeding preference for dandelions (Kogan 1975). Matsuda *et al*. (1993) modeled the effects of multiple predators on antipredator defenses and concluded that increasing defense against one predator comes at the expense of defenses against another. Hence, conflicts of interest among metabolic pathways, strategies, or life stages often reduce overall efficiency of resource use. Resource allocation by insects, as well as other organisms, reflects tradeoffs among alternative strategies, even between life stages.

Heinrich (1979) evaluated the tradeoffs among various allocation strategies seen among bees. Some bee species begin producing queens and drones (offspring) concurrent with colony development (i.e., production of combs and workers), whereas other bee species achieve large colony sizes before producing queens and drones. The first strategy yields immediate, but small, returns because of the competing activities of workers, and the second strategy yields no immediate returns but eventually yields much larger returns. In addition, workers must weigh the cost of foraging from particular flowers against the expected nectar returns, especially at low temperatures when nectar return must be at least sufficient to maintain high thoracic temperatures necessary for continued foraging. Because different flowers provide different amounts of nectar, bees tend to forage at flowers with high yields over a range of temperatures but visit flowers with small nectar rewards only at high temperatures. Similarly, bees must weigh the benefits of foraging at various distances from the colony. Bees will fly several kilometers, given adequate floral rewards, but respond quickly to indications of declining nectar availability (e.g., leave an inflorescence or patch after encountering empty flowers).

Heterogeneous habitats force many herbivores and predators to expend energy searching for scattered resources. Many individuals will be unable to maintain energy or nutrient balance under such conditions. By contrast, abundant suitable resources reduce costs of searching for, or detoxifying, resources and facilitate maintenance of energy and nutrient budgets. Frequent encounters with predators, especially when combined with low availability of food resources, may restrict the time an individual can spend foraging and increase the expenditure of energy to avoid predators, reducing net energy acquisition and potentially leading to inadequate energy balance for survival.

Survival of individuals and species represents the net result of various traits that often conflict (Carrière *et al*. 1997). Environmental changes, especially rapid changes occurring as a result of anthropogenic activities, will change the balance among these tradeoffs, affecting the net result in various ways. Warmer global temperatures may improve energy balance for some arctic species but increase respiration loss or time spent seeking shade for other species. Ecosystem fragmentation will require greater energy expenditure for sufficient foraging and dispersal, thereby impeding movement of intolerant species over inhospitable landscapes. Some species will benefit from changes that improve overall performance (e.g., survival and reproduction), whereas other species will decline or disappear.

IV. SUMMARY

Acquired resources are allocated to various pathways. First, they either are assimilated or egested. Assimilated resources either are allocated to production or are expended (i.e., through respiration). Consumption and allocation of resources are influenced by insect size, maturity, food quality, and parasitism. Fitness accrues to the extent that assimilated resources are used for growth and reproduction. However, insect allocation patterns represent tradeoffs among competing requirements of growth, reproduction, and activities necessary for food acquisition, mating, reproduction, and interactions with other organisms.

Species persist to the extent that the benefits of these behaviors outweigh the costs (i.e., survival and reproduction are increased by the investment of energy in particular behavior and associated biochemicals). Foraging and reproductive behaviors should provide the best return for the time and effort spent searching. Reproductive behavior should maximize survival of offspring. Among insects, selection of appropriate oviposition sites determines egg development and survival. Brood care is well-represented among insects, with examples ranging from protection of young, to provision of food resources, to development of complex social systems for brood care and colony maintenance. However, efficiency of adult behaviors may be in conflict with efficiency of juvenile behaviors. For example, adults may oviposit on the most easily found hosts, whereas survival of immatures may depend on discovery of more suitable food hosts.

Competition and defense against predators often involve considerable expenditure of resources. In many species, males engage in various forms of combat to decide which males mate successfully. Territorial behavior is characterized by both the marking of territorial boundaries and the defense of the territory against intruders. Defense of territories may maximize access to food or mates at low population densities but becomes less advantageous and may be abandoned at high population densities. Insects defend themselves against predators physically and chemically. Behavior often enhances the effectiveness of protective coloration or toxins. For example, cryptically colored insects usually avoid movement during times when predators are active, whereas other insects may suddenly expose eyespots or brightly colored body parts to startle an attacker. Some insects imitate snakes or other predators through color patterns or movements. Such strategies minimize the energetic cost of physical defense but require greater efficiency in foraging or reproductive movements to avoid detection.

The efficiency of foraging, reproductive, competitive, and defensive behavior may be increased by use of visual, chemical, or acoustic signals that communicate information to recipients. Insects can improve foraging and mating efficiency by orienting toward chemical cues produced by suitable resources or potential mates. Discovery of a potential mate initiates a courtship ritual that improves fitness by ensuring species recognition and receptivity. Competition for food or mates can be minimized by signals that deter other individuals.

Environmental changes will affect the efficiency of resource acquisition and allocation strategies. For example, global warming will improve energy balance for some species (e.g., early season or high latitude pollinators) but increase respiration costs beyond ability to acquire energy and nutrients for others. Ultimately, insect strategies for acquiring and allocating energy and nutrient resources affect community interactions, energy flow, and nutrient cycling processes.

SECTION II

POPULATION ECOLOGY

A POPULATION IS A GROUP OF INTERBREEDING MEMBERS of a species. A number of more or less discrete subpopulations may be distributed over the geographic range of a species population. Movement of individuals among these "demes" (composing a "metapopulation") and newly available resources compensate for local extinctions resulting from disturbances or biotic interactions (Hanski and Gilpin 1997). Populations are characterized by structural attributes, such as density; dispersion pattern; and age, sex, and genetic composition (Chapter 5) that change through time (Chapter 6) and space (Chapter 7) as a result of responses to changing environmental conditions.

Population structure and dynamics of insects have been the subject of much ecological research. This is the level of ecological organization that is the focus of evolutionary ecology, ecological genetics, biogeography, development of sampling methods, pest management, and recovery of endangered species. These disciplines all have contributed enormously to our understanding of population-level phenomena.

Abundance of many insects can change orders of magnitude on very short time scales because of their small size and rapid reproductive rates. Such rapid and dramatic change in abundance in response to often-subtle environmental changes facilitates statistical evaluation of population response to environmental factors and makes insects useful indicators of environmental change. The reproductive capacity of many insects enables them to colonize new habitats and exploit favorable conditions or new resources quickly. However, their small size, short life span, and dependence on chemical communication to find mates at low densities limit persistence of small or local populations during periods of adverse conditions, frequently leading to local extinction.

Population dynamics reflect the net effects of differences among individuals in their physiological and behavioral interactions with the environment. Changes in individual success in finding and exploiting resources, mating and reproducing, and avoiding mortality agents determine numbers of individuals, their spatial distribution, and genetic composition at any point in time. Population structure is a component of the environment for the members of the population and provides information that affects individual physiology and behavior, and hence fitness (see Section I). For example, population density affects competition for food and oviposition sites (as well as other resources), propensity of individuals to disperse, and the proximity of potential mates.

Population structure and dynamics also affect community structure and ecosystem processes (Sections III and IV). Each population constitutes a part of the environment for other populations in the community. Changes in abundance of any one species population affect the population(s) on which it feeds and population(s) that prey on, or compete with, it. Changes in size of any population also affect the importance of its ecological functions. A decline in pollinator abundance will reduce fertilization and seed production of host plants, thereby affecting aspects of nutrient uptake and primary productivity. An increase in phytophage abundance can increase canopy “porosity,” increasing light penetration and increasing fluxes of energy, water, and nutrients to the soil. A decline in predator abundance will release prey populations from regulation and contribute to increased exploitation of the prey’s resources. A decline in detritivore abundance can reduce decomposition rate and lead to bottlenecks in biogeochemical cycling that affect nutrient availability.

Population structure across landscapes also influences source-sink relationships that determine population viability and ability to recolonize patches following disturbances. For example, the size and distribution of demes determine their ability to maintain gene flow or to diverge into separate species. Distribution of demes also determines the source(s) and initial genetic composition of colonists arriving at a new habitat patch. These population attributes are critical to protection or restoration of rare or endangered species. Isolation of demes as a result of habitat fragmentation can reduce their ability to reestablish local demes and lead to permanent changes in community structure and ecosystem processes across landscapes.

5

Population Systems

THE VARIABLES THAT DETERMINE THE ABUNDANCE AND DISTRIBUTION of a population, in time and space, constitute a population system (Berryman 1981). The basic elements of this system are the individual members of the population, variables describing population size and structure, processes that affect population size and structure, and the environment. These elements of the population system largely determine the capacity of the population to increase in size and maintain itself within a shifting landscape mosaic of habitable patches. This chapter summarizes these population variables and processes, their integration in life history strategies, and their contribution to change in population size and distribution.

I. POPULATION STRUCTURE

Population structure reflects several variables that describe the number and spatial distribution of individuals and their age, sex, and genetic composition. Population variables reflect life history and the physiological and behavioral attributes that dictate habitat preferences, home ranges, oviposition patterns, and affinity for other members of the population.

A. Density

Population density is the number of individuals per unit geographic area (e.g., number per m^2, per ha, or per km^2). This variable affects a number of other population variables. For example, mean density determines population viability and the probability of colonizing vacant habitat patches. Density also affects population dispersion pattern (see the next section). A related measure, population intensity, is commonly used to describe insect population structure. Intensity is the number of individuals per habitat unit, such as number per leaf, per m branch length, per m^2 leaf area or bark surface, per kg foliage or wood, etc. Mean intensity indicates the degree of resource exploitation; competition for space, food, or mates; and magnitude of effect on ecosystem processes. Intensity measures often can be converted to density measures if the density of habitat units is known (Southwood 1978).

Densities and intensities of insect populations can vary widely. Bark beetles, for example, often appear to be absent from a landscape (very low density) but, with sufficient examination, can be found at high intensities on widely scattered injured or diseased trees or in the dying tops of trees (Schowalter 1985). Under favorable conditions of climate and host abundance and condition, populations of these beetles can reach sizes of up to 10^5 individuals per tree over areas as large as 10^7 ha (Coulson 1979, Furniss and Carolin 1977). Schell and Lockwood (1995) reported that grasshopper population densities can increase an order of magnitude over areas of several thousand hectares within 1 year.

B. Dispersion

Dispersion is the spatial pattern of distribution of individuals. Dispersion is an important characteristic of populations that affects spatial patterns of resource use and population effect on community and ecosystem attributes. Dispersion pattern can be regular, random, or aggregated.

A regular (uniform) dispersion pattern is seen when individuals space themselves at regular intervals within the habitat. This dispersion pattern is typical of species that contest resource use, especially territorial species. For example, bark beetles attacking a tree show a regular dispersion pattern (Fig. 5.1). Such spacing reduces competition for resources. From a sampling perspective, the occurrence of one individual in a sample unit reduces the probability that other individuals will occur in the same sample unit. Variability in mean density is low, and sample densities tend to be normally distributed. Hence, regularly dispersed populations are most easily monitored because a relatively small number of samples provides the same estimates of mean and variance in population density as does a larger number of samples.

In a randomly dispersed population, individuals neither space themselves apart nor are attracted to each other. The occurrence of one individual in a sample unit has no effect on the probability that other individuals will occur in the same sample unit (see Fig. 5.1). Sample densities show a skewed (Poisson) distribution.

Aggregated (or clumped) dispersion results from grouping behavior or restriction to particular habitat patches. Aggregation is typical of species that occur in herds, flocks, schools, etc. (see Fig. 5.1), for enhancement of resource

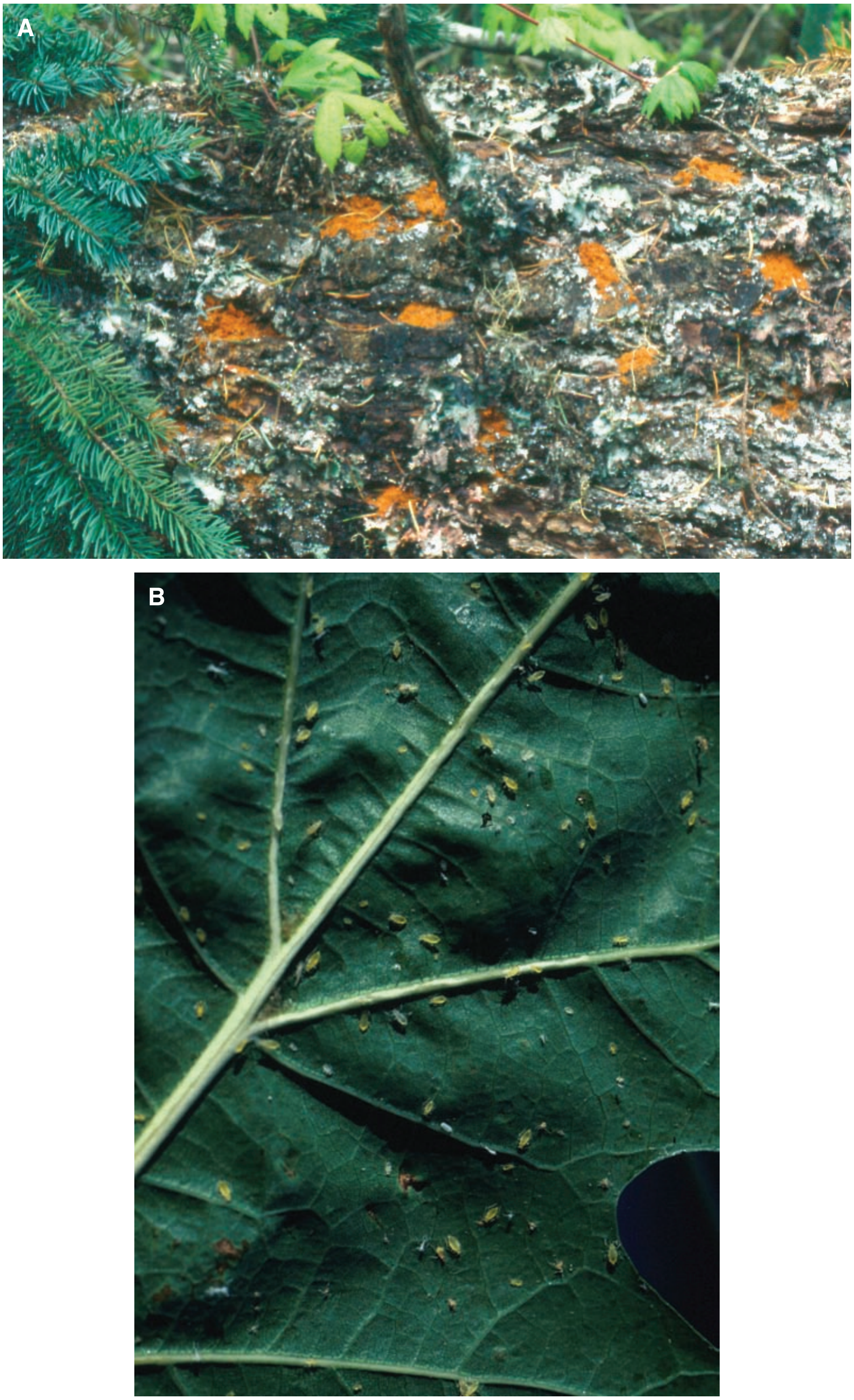


FIG. 5.1 Dispersion patterns and their frequency distributions. **A:** Regular dispersion of Douglas-fir beetle entrances (marked by the small piles of reddish phloem fragments) through bark on a fallen Douglas-fir tree. **B:** Random dispersion of aphids on an oak leaf. **C:** Aggregated dispersion of overwintering ladybird beetles on a small shrub in a forest clearing.

FIG. 5.1 (*Continued*)

exploitation or protection from predators (see Chapter 3). Gregarious sawfly larvae and tent caterpillars are examples of aggregated dispersion resulting from tendency of individuals to form groups (see Fig. 2.12). Filter-feeding aquatic insects tend to be aggregated in riffles or other zones of higher flow rate within the stream continuum (e.g., Fig. 2.14), whereas predators that hide in benthic detritus, such as dragonfly larvae or water scorpions, are aggregated in pools as a result of their habitat preferences. Aphids may be aggregated as a result of rapid, parthenogenic reproduction, as well as host and habitat preferences. Massonnet *et al.* (2002) found that the aphid *Macrosiphoniella tanacetaria*, a specialist on tansy, *Tanacetum vulgare*, can be aggregated at the level of individual shoots, plants, and sites.

For sampling purposes, the occurrence of an individual in a sample unit increases the probability that additional individuals occur in that sample unit. Sample densities are distributed as a negative binomial function, and variance tends to be high. Populations with this dispersion pattern require the greatest number of samples and attention to experimental design. A large number of samples is necessary to minimize the obviously high variance in numbers of individuals among sample units and to ensure adequate representation of aggregations. A stratified experimental design can facilitate adequate representation with smaller sample sizes if the distribution of aggregations among different habitat types is known.

Dispersion pattern can change during insect development, during change in population density, or across spatial scales. For example, larval stages of tent caterpillars and gregarious sawflies are aggregated at the plant branch level, but adults are randomly dispersed at this scale (Fitzgerald 1995, McCullough and Wagner 1993). Many host-specific insects are aggregated on particular hosts in diverse communities but are more regularly or randomly dispersed in more homogeneous communities dominated by hosts. Some insects, such as the western ladybird beetle, *Hippodamia convergens*, aggregate for overwintering purposes and redisperse in the spring. Aphids are randomly dispersed at low population densities but become more aggregated as scattered colonies increase in size (Dixon 1985). Bark beetles show a regular dispersion pattern on a tree bole, as a result of spacing behavior, but are aggregated on injured or diseased trees (Coulson 1979).

C. Metapopulation Structure

The irregular distribution of many populations across landscapes creates a pattern of relatively distinct (often isolated) local demes (aggregations) that compose the greater metapopulation (Hanski and Gilpin 1997). Insect species characterizing discrete habitat types often are dispersed as relatively distinct local demes as a result of environmental gradients or disturbances that affect the distribution of habitat types across the landscape. Obvious examples include insects associated with lotic or high-elevation ecosystems. Populations of insects associated with ponds or lakes show a dispersion pattern reflecting dispersion of their habitat units. Demes of lotic species are more isolated in desert ecosystems than in mesic ecosystems. Populations of western spruce budworm, *Choristoneura occidentalis*, and fir engraver beetle, *Scolytus ventralis*, historically occurred in western North America in relatively isolated high elevation and riparian fir forests separated by more xeric patches of pine forest (Wickman 1992).

Metapopulations usually are composed of demes of various sizes, reflecting the size or quality, or both, of habitat patches. For example, Leisnham and Jamieson (2002) found that demes of mountain stone weta, *Hemideina maori*, which shelter under rocks on isolated rock outcrops (tor) in alpine habitats in southern New Zealand, ranged in size from 0 to 6 adults on tors with 1–12 rocks and from 15 to 40 adults on tors with 30–40 rocks. Small tors were more likely to experience extinction events (4 of 14 small tors experienced at least 1 extinction during the 3-year study) than were large tors (no extinction events during the study).

Population structure among suitable patches is influenced strongly by the matrix of patch types. Haynes and Cronin (2003) studied the distribution of planthoppers, *Prokelisia crocea*, among discrete patches of prairie cordgrass, *Spartina pectinata*, as affected by surrounding mudflat, native nonhost grasses, or exotic smooth brome (*Bromus inermis*). Planthoppers were released into experimental cordgrass patches constructed to be identical in size (about 24 × 24 cm), isolation (>25 m from natural cordgrass patches), and host plant quality. Within patches, planthopper density was higher against mudflat edges, relative to patch interior, but not against nonhost patches. Among patches, density increased with increasing proportion of surrounding matrix composed of mudflat. The influence of matrix composition was equal to the influence of patch size and isolation in explaining planthopper distribution.

Population distribution and degree of isolation among local demes affect gene structure and viability of the metapopulation. If local demes become too isolated, they become inbred and may lose their ability to recolonize habitable patches following local extinction (Hedrick and Gilpin 1997). As human activities increasingly fragment natural ecosystems, local demes become isolated more rapidly than greater dispersal ability can evolve, and species extinction becomes more likely. These effects of fragmentation could be exacerbated by climate change. For example, a warming climate will push high-elevation ecosystems into smaller areas on mountaintops, and some mountaintop ecosystems will disappear (Fig. 5.2) (Franklin *et al.* 1992, D. Williams and Liebhold 2002). Rubenstein (1992) showed that individual tolerances to temperature changes could affect range changes by insects under warming climate scenarios. A species with a linear response to temperature could extend its range to higher latitudes (provided that expansion is not limited by habitat fragmentation) without reducing its current habitat. Conversely, a species with a dome-shaped response to temperature could extend into higher latitudes but would be forced to retreat from lower latitudes that become too warm. If the pathway for range adjustment for this species was blocked by unsuitable habitat, it would face extinction. Metapopulation dynamics are discussed in more detail in Chapter 7.

D. Age Structure

Age structure reflects the proportions of individuals at different life stages. This variable is an important indicator of population status. Growing populations generally have larger proportions of individuals in younger age-classes, whereas declining populations usually have smaller proportions of individuals in these age classes. Stable populations usually have relatively more individuals in reproductive age-classes. However, populations with larger proportions of individuals in younger age-classes also may reflect low survivorship in these age classes, whereas populations with smaller proportions of individuals in younger age-classes may reflect high survivorship (see later in this chapter).

For most insect species, life spans are short (usually ≦1 year) and revolve around seasonal patterns of temperature and rainfall. Oviposition usually is timed to ensure that feeding stages coincide with the most favorable seasons and that diapausing stages occur during unfavorable seasons (e.g., winter in temperate regions and dry season in tropical and arid regions). Adults usually die after reproducing. Although there are many exceptions, most temperate species have discrete, annual generations, whereas tropical species are more likely to have overlapping generations.

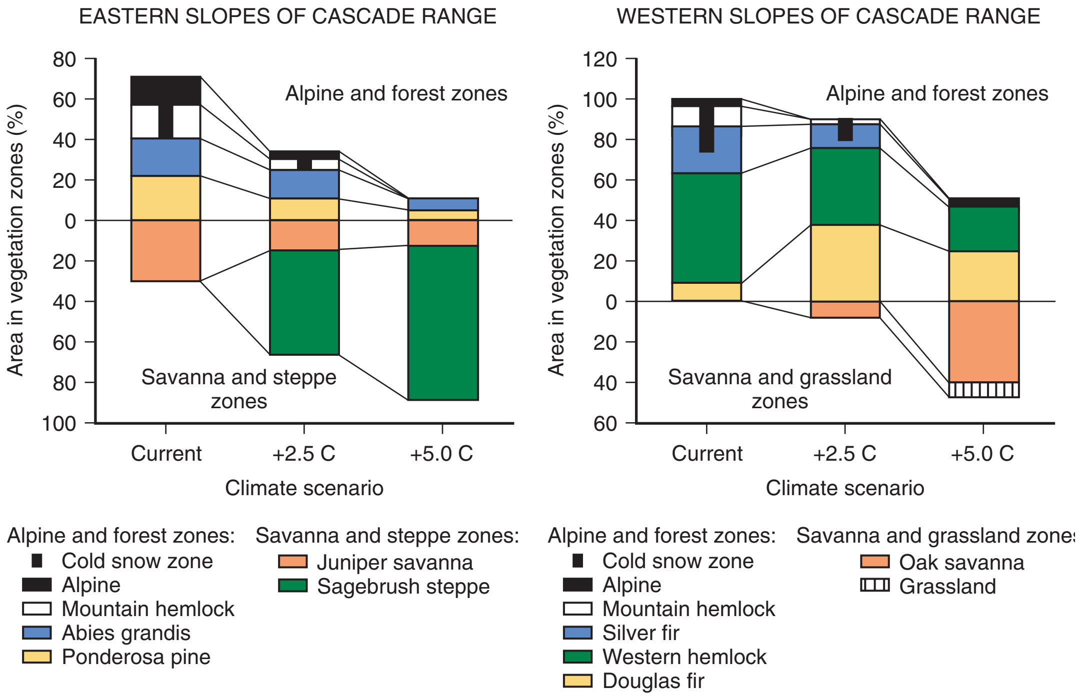


FIG. 5.2 Changes in the percentage area in major vegetation zones on the eastern (*left*) and western (*right*) slopes of the Cascade Range in Oregon as a result of temperature increases of 2.5°C and 5°C. Major changes are predicted in elevational boundaries and total area occupied by vegetation zones under these global climate change scenarios. Vegetation zones occupying higher elevations will decrease in area or disappear as a result of the smaller conical surface at higher elevations. Other species associated with vegetation zones also will become more or less abundant. From Franklin *et al.* (1992) with permission of Yale University Press.

E. Sex Ratio

The proportion of females indicates the reproductive potential of a population. Sex ratio also reflects a number of life history traits, such as the importance of sexual reproduction, mating system, and ability to exploit harsh or ephemeral habitats (Pianka 1974).

A 50 : 50 sex ratio generally indicates equally important roles of males and females, given that selection would minimize the less-productive sex. Sex ratio approaches 50 : 50 in species where males select resources, protect or feed females, or contribute necessary genetic variability. This sex ratio maximizes availability of males to females and, hence, maximizes genetic heterogeneity. High genetic heterogeneity is particularly important for population survival in heterogeneous environments. However, when the sexes are equally abundant, only half of the population is capable of producing offspring. By contrast, a parthenogenetic population (with no males) has little or no genetic heterogeneity, but the entire population is capable of producing offspring. Parthenogenetic individuals can disperse and colonize new resources without the additional challenge of finding mates, and successful colonists can generate large population sizes rapidly, ensuring exploitation of suitable resources and large numbers of dispersants in the next generation.

Sex ratio can be affected by environmental factors. For example, haploid males of many insect species are more sensitive to environmental variation than are diploid females, and greater mortality to haploid males may speed adaptation to changing conditions by quickly eliminating deleterious genes (Edmunds and Alstad 1985, J. Peterson and Merrell 1983).

F. Genetic Composition

All populations show variation in genetic composition (frequencies of various alleles) among individuals and through time. The degree of genetic variability and the frequencies of various alleles depend on a number of factors, including mutation rate, environmental heterogeneity, and population size and mobility (Hedrick and Gilpin 1997, Mopper 1996, Mopper and Strauss 1998). Genetic variation may be partitioned among isolated demes or affected by patterns of habitat use (Hirai *et al.* 1994). Genetic structure, in turn, affects various other population parameters, including population viability (Hedrick and Gilpin 1997).

Populations vary in the frequency and distribution of various alleles. Widespread species might be expected to show greater variation across their geographic range than would more restricted species. Roberds *et al.* (1987) measured genetic variation from local to regional scales for the southern pine beetle, *Dendroctonus frontalis*, in the southeastern United States. They reported that allelic frequencies were somewhat differentiated among populations from Arkansas, Mississippi, and North Carolina but that a population in Texas was distinct. They found little or no variation among demes within each state and evidence of considerable inbreeding among beetles at the individual tree level.

Roberds *et al.* (1987) also reported that only 1 allele of the 7 analyzed showed significant variation between demes that were growing and colonizing new trees and demes not growing or colonizing new trees. The genetic variation of the founders of a new deme is relatively low, simply because of the small number of colonists and the limited proportion of the gene pool that they represent. Colonists from a population with low genetic variability start a population with even lower genetic variability (Hedrick and Gilpin 1997). Therefore, the size and genetic variability of the source populations, as well as the number of colonists, determine genetic variability in founding populations. Genetic variability remains low during population growth unless augmented by new colonists. This is especially true for parthenogenetic species, such as aphids, for which an entire population could represent clones derived from a founding female. Differential dispersal ability among genotypes affects heterozygosity of colonists. Florence *et al.* (1982) reported that the frequencies of 4 alleles for an esterase (esB) converged in southern pine beetles collected along a 150-m transect extending from an active infestation in east Texas. As a result, heterozygosity increased significantly with distance, approaching the theoretical maximum of 0.75 for a gene locus with 4 alleles. These data suggested a system that compensates for loss of genetic variability as a result of inbreeding by small founding populations and maximizes genetic variability in new populations coping with different selection regimens (Florence *et al.* 1982). Nevertheless, dispersal among local populations is critical to maintaining genetic variability (Hedrick and Gilpin 1997). If isolation restricts dispersal and infusion of new genetic material into local demes, inbreeding may reduce population ability to adapt to changing conditions, and recolonization following local extinction will be more difficult.

Polymorphism occurs commonly among insects and may underlie their rapid adaptation to environmental change or other selective pressures, such as predation (A. Brower 1996, Sheppard *et al.* 1985). Among the best-known examples of population response to environmental change is the industrial melanism that developed in the peppered moth, *Biston betularia*, in England following the industrial revolution (Kettlewell 1956). Selective predation by insectivorous birds was the key to the rapid shift in dominance from the white form, which is cryptic on light surfaces provided by lichens on tree bark, to the black form, which is more cryptic on trees blackened by industrial effluents. Birds preying on the more conspicuous morph maintained low frequencies of the black form in preindustrial England, but later they greatly reduced frequencies of the white form. Other examples of polymorphism also appear to be maintained by selective predation. In some cases, predators focusing on inferior Müllerian mimics of multiple sympatric models may select for morphs or demes that mimic different models (e.g., A. Brower 1996, Sheppard *et al.* 1985).

Genetic polymorphism can develop in populations that use multiple habitat units or resources (Mopper 1996, Mopper and Strauss 1998, Via 1990). Sturgeon and Mitton (1986) compared allelic frequencies among mountain pine beetles, *Dendroctonus ponderosae*, collected from three pine hosts [ponderosa (*Pinus ponderosa*), lodgepole (*P. contorta*), and limber (*P. flexilis*)] at each of five sites in Colorado. Significant variation occurred in morphological traits and allelic frequencies at five polymorphic enzyme loci among the five populations and among the three host species, suggesting that the host species is an important contributor to genetic structure of polyphagous insect populations.

Via (1991a) compared the fitnesses (longevity, fecundity, and capacity for population increase) of pea aphid, *Acyrthosiphon pisum*, clones from two host plants (alfalfa and red clover) on their source host or the alternate host. She reported that aphid clones had higher fitnesses on their source host, compared to the host to which they were transplanted, indicating local adaptation to factors associated with host conditions. Furthermore, significant negative correlations for fitness between source host and alternate host indicated increasing divergence between aphid genotypes associated with different hosts. In a subsequent study, Via (1991b) evaluated the relative importance of genetics and experience on aphid longevity and fecundity on source and alternate hosts. She maintained replicate lineages of the two clones (from alfalfa versus clover) on both host plants for three generations, then tested performance of each lineage on both hosts. If genetics is the more important factor affecting aphid performance on source and alternate host, then aphids should have highest fitness on the host to which they were adapted, regardless of subsequent rearing on the alternate host. However, if experience is the more important factor, then aphids should have highest fitness on the host from which they were reared. Via found that three generations of experience on the alternate host did not significantly improve fitness on that host. Rather, fitness was highest on the plant from which the clone was derived originally, supporting the hypothesis that genetics is the more important factor. These data indicated that continued genetic divergence of the two subpopulations is likely, given that individuals dispersing between alternate hosts cannot improve their performance through time as a result of experience.

Biological factors that determine mate selection or mating success also affect gene frequencies, perhaps in concert with environmental conditions. In a laboratory experiment with sex-linked mutant genes in *Drosophila melanogaster* (Peterson and Merrell 1983), mutant and wild-male phenotypes exhibited about the same viability, but mutant males showed a significant mating disadvantage, leading to rapid elimination (i.e., within a few generations) of the mutant allele. In addition, whereas the wild-male phenotype tended to show a rare male advantage in mating (i.e., a higher proportion of males mating at low relative abundance), mutant males showed a rare male disadvantage (i.e., a lower proportion of males mating at low relative abundance), increasing their rate of elimination. Malausa *et al.* (2005) used a combination of genetic and stable isotope (^{13}C) techniques to identify host plant sources of 396 male and 393 female European corn borer, *Ostrinia nubilalis*, collected at multiple sites, and of 535 spermatophores carried by these females, over a 2-year period (2002–2003). Moths could be differentiated unambiguously on the basis of larval host, either C_3 or C_4 plants. All but 5 females (3 in 2002 and 2 in 2003) had mated with a male from the same host race, indicating >95 assortative mating. These data indicate that nonrandom mating patterns can lead to rapid changes in gene frequencies among diverging races from different hosts.

Insect populations can adapt to environmental change more rapidly than can longer-lived, more slowly reproducing, organisms (Mopper 1996, Mopper and Strauss 1998). Heterogeneous environmental conditions tend to mitigate directional selection: any strong directional selection by any environmental factor during one generation can be modified in subsequent generations by a different prevailing factor. However, changes in genetic composition occur quickly in insects when environmental change does impose directional selective pressure, such as in the change from preindustrial to postindustrial morphotypes in the polymorphic peppered moth (Kettlewell 1956).

The shift from pesticide-susceptible to pesticide-resistant genotypes may be particularly instructive. Selective pressure imposed by insecticides caused rapid development of insecticide-resistant populations for many species. Resistance development is facilitated by the widespread occurrence in insects, especially herbivores, of genes that encode for enzymes that detoxify plant defenses because ingested insecticides also are susceptible to detoxification by these enzymes. Although avoidance of directional selection for resistance to any single tactic is a major objective of integrated pest management (IPM), pest management in practice still involves widespread use of the most effective tactic. Following the appearance of transgenic insect-resistant crop species in the late 1980s, genetically engineered, Bt toxin-producing corn, cotton, soybeans, and potatoes have replaced nontransgenic varieties over large areas, raising concern that these crops might quickly select for resistance in target species (Alstad and Andow 1995, Tabashnik 1994, Tabashnik *et al.* 1996).

Laboratory studies have shown that at least 16 species of Lepidoptera, Coleoptera, and Diptera are capable of developing resistance to the Bt gene as a result of strong selection (Tabashnik 1994). However, few species have shown resistance in the field. The diamondback moth, *Plutella xylostella*, has shown resistance to Bt in field populations from the United States, Philippines, Malaysia, and Thailand. Resistance in some species has been attributed to reduced binding of the toxin to membranes of the midgut epithelium. A single gene confers resistance to four Bt toxins in the diamondback moth (Tabashnik *et al.* 1997), and >5000-fold resistance can be achieved in a few generations (Tabashnik *et al.* 1996). Resistance can be reversed when exposure to Bt toxin is eliminated for several generations, probably because of fitness costs of resistance (Tabashnik *et al.* 1994), but some strains can maintain resistance in the absence of Bt for more than 20 generations (Tabashnik *et al.* 1996).

Resistance development in the field can be minimized by alternating control strategies to prevent strong directional selection in exposed populations. In particular, a strategy of high Bt concentration in transgenic crops, together with nontransgenic refuges, has been successful both in reducing use of conventional insecticides and in preventing resistance development (Alstad and Andow 1995, Carrière *et al.* 2001b, 2003). High concentration of Bt minimizes survivorship on the transgenic crop, and greater survivorship in the nontransgenic crop prevents fixation of resistance genes in the population (see Chapter 16).

G. Social Insects

Social insects pose some special problems for description of population structure. On the one hand, each individual requires resources and contributes to interactions with other organisms. On the other hand, colony member activity is centered on the nest, and collective foraging territory is defined by proximity to surrounding colonies. Furthermore, food transfer among nestmates (trophallaxis) supports a view of colonies as sharing a collective gut. Hence, each colony appears to function as an ecological unit, with colony size (number of members) determining its individual physiology and behavior. For some social insects, the number of colonies per ha may be a more useful measure of density than is number of individuals per ha.

However, defining colony boundaries and distinguishing between colonies may be problematic for many species, especially those with underground nests. Molecular techniques have proved to be a valuable tool for evaluating relatedness within and among colonies in an area.

Colonies of social Hymenoptera can be monogyne (having one queen) or polygyne (having multiple queens), with varying degrees of relatedness among queens and workers (Pamilo *et al.* 1997). Intracolonial relatedness can vary among colonies and among populations. In some ants, such as *Solenopsis invicta* and some *Formica* species, social polymorphism can be observed, with distinct monogynous (M type) and polygynous (P type) colonies. The two types generally show high relatedness to each other where they occur in the same area. However, gene flow is restricted in the polygynous type and between monogynous and polygynous types. Populations of polygynous colonies generally are more genetically differentiated than are those of monogynous colonies in the same area (Pamilo *et al.* 1997).

Polygyny may be advantageous in areas of intense competition, where the more rapid reproduction by multiple queens may confer an advantage, regardless of the relatedness of the queens. However, additional queens eventually may be eliminated, especially in ant species, with workers often favoring queens on the basis of size or condition rather than which queen is mother to most workers (Pamilo *et al.* 1997).

Similarly, termite colonies are cryptic and may have variable numbers of reproductive adults. Husseneder and Grace (2001b) and Husseneder *et al.* (1998) found DNA (deoxyribonucleic acid) fingerprinting to be more reliable than aggression tests or morphometry for distinguishing termites from different colonies or sites. As expected, genetic similarity is higher among termites within collection sites than between collection sites (Husseneder and Grace 2001a, Husseneder *et al.* 1998). Moderate inbreeding often is evident within termite colonies, but low levels of genetic differentiation at regional scales suggest that substantial dispersal of winged adults homogenizes population genetic structure (Husseneder *et al.* 2003). However, several species are polygynous and may show greater within-colony genetic variation, depending on the extent to which multiple reproductives are descended from a common parent (Vargo *et al.* 2003). Kaib *et al.* (1996) found that foraging termites tended to associate with close kin in polygynous and polyandrous colonies of *Schedorhinotermes lamanianus*, leading to greater genetic similarity among termites within foraging galleries than at the nest center.

Genetic studies have challenged the traditional view of the role of genetic relatedness in the evolution and maintenance of eusociality. Eusociality in the social Hymenoptera has been explained by the high degree of genetic relatedness among siblings, which share 75% of their genes as a result of haploid father and diploid mother, compared to only 50% genes shared with their mother (Hamilton 1964, See Chapter 15). However, this model does not apply to termites. Husseneder *et al.* (1999) and Thorne (1997) suggested that developmental and ecological factors, such as slow development, iteroparity, overlap of generations, food-rich environment, high risk of dispersal, and group defense, may be more important than genetics in the maintenance of termite eusociality, regardless of the factors that may have favored its original development. Myles (1999) reviewed the frequency of neoteny (reproduction by immature stages) among termite species and concluded that neoteny is a primitive element of the caste system that may have reduced the fitness cost of not dispersing, leading to further differentiation of castes and early evolution of eusociality.

II. POPULATION PROCESSES

The population variables described in the preceding section change as a result of variable reproduction, movement, and death of individuals. These individual contributions to population change are integrated as three population processes: natality (birth rate), mortality (death rate), and dispersal (rate of movement of individuals into or out of the population). For example, density can increase as a result of increased birth rate, immigration, or both; frequencies of various alleles change as a result of differential reproduction, survival, and dispersal. The rate of change in these processes determines the rate of population change, described in the next chapter. Therefore, these processes are fundamental to understanding population responses to changing environmental conditions.

A. Natality

Natality is the population birth rate (i.e., the per capita production of new individuals per unit time). Realized natality is a variable that approaches potential natality—the maximum reproductive capacity of the population—only under ideal environmental conditions. Natality is affected by factors that influence production of eggs (fecundity) or production of viable offspring (fertility) by individual insects. For example, resource quality can affect the numbers of eggs produced by female insects (R. Chapman 1982). Ohgushi (1995) reported that females of the herbivorous ladybird beetle, *Henosepilachna niponica*, feeding on the thistle, *Cirsium kagamontanum*, resorbed eggs in the ovary when leaf damage became high. Female blood-feeding mosquitoes often require a blood meal before first or subsequent oviposition can occur (R. Chapman 1982); the ceratopogonid, *Culicoides barbosai*, produces eggs in proportion to the size of the blood meal (Linley 1966). Hence, poor quality or insufficient food resources can reduce natality. Inadequate numbers of males can reduce fertility in sparse populations. Similarly, availability of suitable oviposition sites also affects natality.

Natality usually is higher at intermediate population densities than at low or high densities. At low densities, difficulties in attracting mates may limit mating, or may limit necessary cooperation among individuals, as in the case of bark beetles that must aggregate to overcome host tree defenses prior to oviposition (Berryman 1981). At high densities, competition for food, mates, and oviposition sites reduces fecundity and fertility (e.g., Southwood 1975, 1977). The influence of environmental conditions can be evaluated by comparing realized natality to potential natality (e.g., estimated under laboratory conditions).

Differences among individual fitnesses are integrated in natality. Differential reproduction among genotypes in the population determines the frequency of various alleles in the filial generation. As discussed earlier in this chapter, gene frequencies can change dramatically within a relatively short time, given strong selection and the short generation times and high reproductive capacity of insects.

B. Mortality

Mortality is the population death rate (i.e., the per capita number of individuals dying per unit time). As with natality, we can distinguish a potential longevity or lifespan, resulting only from physiological senescence, from the realized longevity, resulting from the action of mortality factors. Hence, mortality can be viewed both as reducing the number of individuals in the population and as reducing survival. Both have importance consequences for population dynamics.

Organisms are vulnerable to a variety of mortality agents, including unsuitable habitat conditions (e.g., extreme temperature or water conditions), toxic or unavailable food resources, competition, predation (including cannibalism), parasitism, and disease (see Chapters 2–4). These factors are a focus of studies to enhance pest management efforts. Death can result from insufficient energy or nutrient acquisition to permit detoxification of, or continued search for, suitable resources. Life stages are affected differentially by these various mortality agents (e.g., Fox 1975b, Varley *et al.* 1973). For example, immature insects are particularly vulnerable to desiccation during molts, whereas flying insects are more vulnerable to predation by birds or bats. Many predators and parasites selectively attack certain life stages. Among parasitic Hymenoptera, species attacking the same host have different preferences for host egg, larval, or pupal stages. Predation also can be greater on hosts feeding on particular plant species, compared to other plant species, based on differential toxin sequestration, or predator attraction to plant volatiles (Stamp 1992, Traugott and Stamp 1996, Turlings *et al.* 1990, 1995).

In general, mortality resulting from predation tends to peak at intermediate population densities, when density is sufficient for a high rate of encounter with predators and parasites, but prior to predator satiation (Fig. 5.3) (Southwood 1975, 1977, see Chapter 8). Mortality resulting from competition and canni-

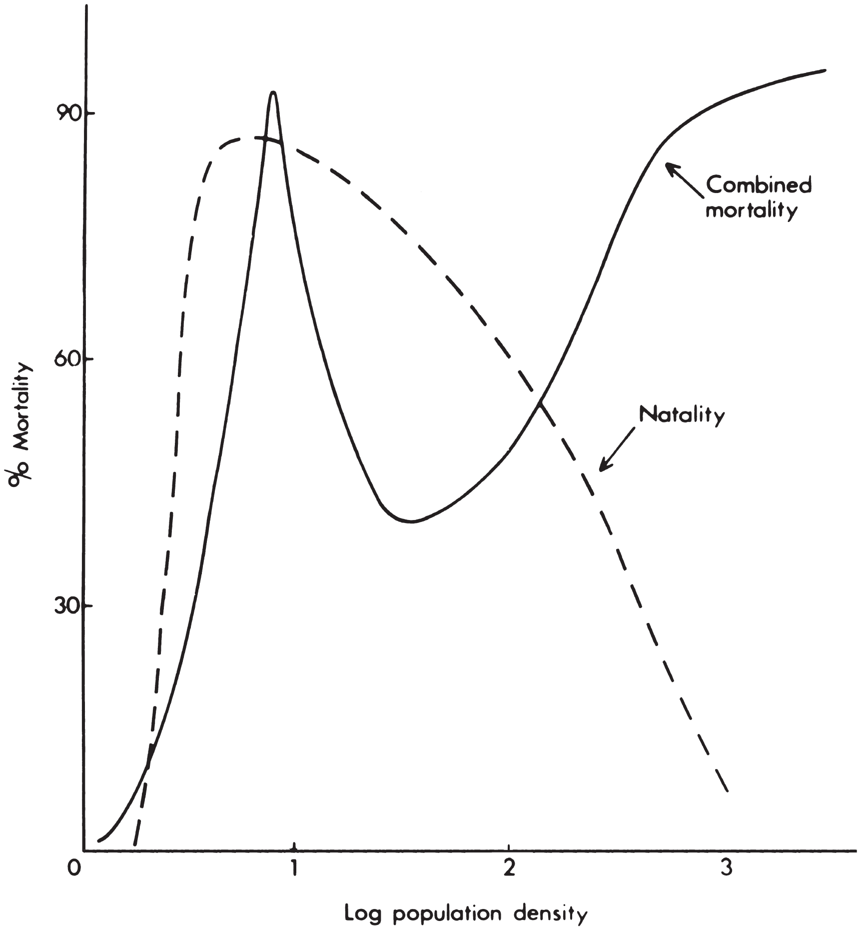


FIG. 5.3 Relationship between population density, natality, and mortality caused by predators and parasites (peaking at lower population density) and interspecific competition (peaking at higher population density). From Southwood (1975). Please see extended permission list pg 570.

balism increases at higher population densities (see Fig. 5.3) (Fox 1975a, b, Southwood 1975, 1977). Competition may cause mortality through starvation, cannibalism, increased disease among stressed individuals, displacement of individuals from optimal habitats, and increased exposure and vulnerability to predation as a result of displacement or delayed development.

Survival rate represents the number of individuals still living in relation to time. These individuals continue to feed and reproduce, thereby contributing most to population size as well as to genetic and ecological processes. Hence, survival rate is an important measure in studies of populations.

Survivorship curves reflect patterns of mortality and can be used to compare the effect of mortality in different populations. Lotka (1925) pioneered the comparison of survivorship curves among populations by plotting the log of number or percent of living individuals against time. Pearl (1928) later identified three types of survivorship curves based on the log of individual survival through time

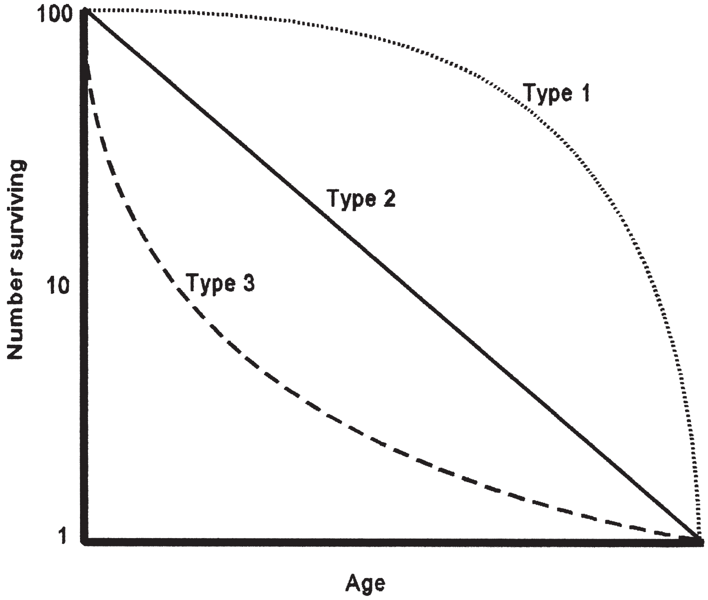


FIG. 5.4 Three generalized types of survivorship curves. Type 1 represents species with high survival rates maintained through the potential life span. Type 2 represents species with relatively constant survivorship with age. Type 3 represents species with low survival rates during early stages but relatively high survival of individuals reaching more advanced ages.

(Fig. 5.4). Type 1 curves represent species, including most large mammals, but also starved *Drosophila* (Price 1997), in which mortality is concentrated near the end of the maximum life span. Type 2 curves represent species in which the probability of death is relatively constant with age, leading to a linear decline in survivorship. Many birds and reptiles approach the Type 2 curve. Type 3 curves are seen for most insects, as well as many other invertebrates and fish, which have high rates of mortality during early life stages but relatively low mortality during later life stages (Begon and Mortimer 1981, Pianka 1974). Species representing Type 3 survivorship must have very high rates of natality to ensure that some offspring reach reproductive age, compared to Type 1 species, which have a high probability of reaching reproductive age.

The form of the survivorship curve can change during population growth. Mason and Luck (1978) showed that survivorship curves for the Douglas-fir tussock moth, *Orgyia pseudotsugata*, changed with population growth from stable to increasing, then decreasing. Survivorship decreased less steeply during population growth and decreased more steeply during population decline, compared to stable populations.

As described for natality, mortality integrates the differential survival among various genotypes, the basis for evolution. Survivors live longer and have greater capacity to reproduce. Hence, selective mortality can alter gene frequencies rapidly in insect populations.

C. Dispersal

Dispersal is the movement of individuals away from their source and includes *spread*, the local movement of individuals, and *migration*, the cyclic mass movement of individuals among areas (L. Clark *et al.* 1967, Nathan *et al.* 2003). As discussed in Chapter 2, long-distance dispersal maximizes the probability that habitat or food resources created by environmental changes or disturbances are colonized before the source population depletes its resources or is destroyed by disturbance. However, dispersal also contributes to infusion of new genetic material into populations. This contribution to genetic heterogeneity enhances population capacity to adapt to changing conditions.

Dispersal incorporates emigration, movement away from a source population, and immigration, movement of dispersing individuals into another population or vacant habitat. Immigration adds new members to the population, or founds new demes, whereas emigration reduces the number of individuals in the population.

Effective dispersal, the number of individuals that successfully immigrate or found new demes, is the product of source strength (the number of individuals dispersing) and the individual probability of success (Nathan *et al.* 2003, Price 1997, see Chapter 2). Source strength is a function of population size, density, and life history strategy. Individual probability of successful dispersal is determined by dispersal mechanism, individual capacity for long-distance dispersal, the distance between source and sink (destination), patch size, and habitat heterogeneity, as described later in this section (see also Chapters 2 and 7).

Species characterizing ephemeral habitats or resources have adapted a greater tendency to disperse than have species characterizing more stable habitats or resources. For example, species found in vernal pools or desert playas tend to produce large numbers of dispersing offspring before water level begins to decline. This ensures that other suitable ponds are colonized and buffers the population against local extinctions. Some dispersal-adapted species produce a specialized morph for dispersal. The dispersal form of most aphids and many scale insects is winged, whereas the feeding form usually is wingless and sedentary. Migratory locusts develop into a specialized long-winged morph for migration, distinct from the shorter-winged nondispersing morph. Some mites have dispersal stages specialized for attachment to phoretic hosts (e.g., ventral suckers in the hypopus of astigmatid mites and anal pedicel in uropodid mites) (Krantz 1978).

Some species have obligatory dispersal prior to reproduction. Cronin and Strong (1999) reported that parasitoid wasps, *Anagrus sophiae*, laid >84% of their eggs in host planthoppers, *Prokelisia* spp., on cordgrass, *Spartina alterniflora*, plants isolated at 10–250 m from source populations.

Dispersal increases with population size or density. Cronin (2003) found that emigration of planthoppers, *Prokelisia crocea*, increased linearly with density of female conspecifics. Crowding increases competition for resources and may interfere with foraging or mating activity, thereby encouraging individuals to seek less-crowded conditions. Leisnham and Jamieson (2002) reported that more mountain stone weta emigrated from large tors with larger demes, but proportionately more weta emigrated from small tors, likely reflecting the greater perimeter-to-area ratio of small tors.

The mating status of dispersing individuals determines their value as founders when they colonize new resources. Clearly, if unmated individuals must find a mate to reproduce after finding a habitable patch, their value as founders is negligible. For some species, mating occurs prior to dispersal of fertilized females (Mitchell 1970). In species capable of parthenogenetic reproduction, fertilization is not required for dispersal and successful founding of populations. Some species ensure breeding at the site of colonization, such as through long-distance attraction via pheromones (e.g., by bark beetles; Raffa *et al.* 1993), or through males accompanying females on phoretic hosts (e.g., some mesostigmatid mites; Springett 1968) or mating swarms (e.g., eastern spruce budworm, *Choristoneura fumiferana*; Greenbank 1957).

Habitat conditions affect dispersal. Individuals are more likely to move greater distances when resources are scarce than when resources are abundant. Furthermore, the presence of predators may encourage emigration (Cronin *et al.* 2004). However, Seymour *et al.* (2003) found that a lycaenid butterfly, *Plebejus argus*, whose larvae are tended by ants, *Lasius niger*, apparently are able to orient toward patches occupied by *L. niger* colonies. Butterfly persistence in patches was influenced more strongly by ant presence than by floral resource density.

Dispersal mechanism determines the likelihood that individuals will reach a habitable patch. Individuals that disperse randomly have a low probability of colonizing a habitable destination. Larval settlement rates for black flies, *Simulium vittatum*, are lowest in the high stream velocity habitats preferred by the larvae as a result of constraints on larval ability to control direction of movement at high flow rates (D. Fonseca and Hart 2001). Conversely, individuals that can control direction of movement and orient toward cues indicating suitable resources have a higher probability of reaching a habitable destination. Transportation by humans has substantially increased possibilities for long-distance dispersal across regional and continental barriers.

The capacity of individuals for long-distance dispersal is determined by flight capacity, nutritional status, and parasitism. Winged insects disperse greater distances than wingless species (Leisnham and Jamieson 2002). Individuals feeding on adequate resources can store sufficient energy and nutrients to live longer and travel farther than can individuals feeding on marginal or inadequate resources. Although dispersal should increase as population density increases, increased competition for food may limit individual energy reserves and endurance at high densities. Furthermore, parasitized individuals may lose body mass more quickly during dispersal than do unparasitized individuals and consequently exhibit shorter flight distances and slower flight speeds (Bradley and Altizer 2005). Hence, dispersal may peak before increasing density and disease reach levels that interfere with dispersal capacity (Leonard 1970, Schowalter 1985).

Dispersing individuals become vulnerable to new mortality factors. Whereas nondispersing individuals may be relatively protected from temperature extremes and predation through selection of optimal microsites, dispersing individuals are exposed to ambient temperature and humidity, high winds, and predators as they move across the landscape. Exposure to higher temperatures increases metabolic rate and depletes energy reserves more quickly, reducing the time and distance an insect can travel (Pope *et al.* 1980). Actively moving insects also are more conspicuous and more likely to attract the attention of predators (Schultz 1983). Dispersal across inhospitable patches may be inhibited or ineffective (Haynes and Cronin 2003). However, insects in patches with high abundance of predators may be induced to disperse as a result of frequent encounters with predators (Cronin *et al.* 2004).

The number of dispersing individuals declines with distance from the source population, with the frequency distribution of dispersal distances often described by a negative exponential or inverse power law (Fig. 5.5). However, some species show a higher proportion of long-distance dispersers than would be expected from a simple diffusion model, suggesting heterogeneity in dispersal type (Cronin *et al.* 2000). A general functional model of dispersal (D) can be described by the following equation:

$$D = \frac{c}{2\alpha\Gamma(1/c)} \exp\left(-\frac{|x|}{|\alpha|}^{c}\right) \tag{5.1}$$

where c and α are shape and distance parameters, respectively, and Γ(1/c) is the gamma function (J. Clark *et al.* 1998, Nathan *et al.* 2003). The negative exponential (c = 1) and Gaussian (c = 2) are special cases of this formula. Similarly, effec-

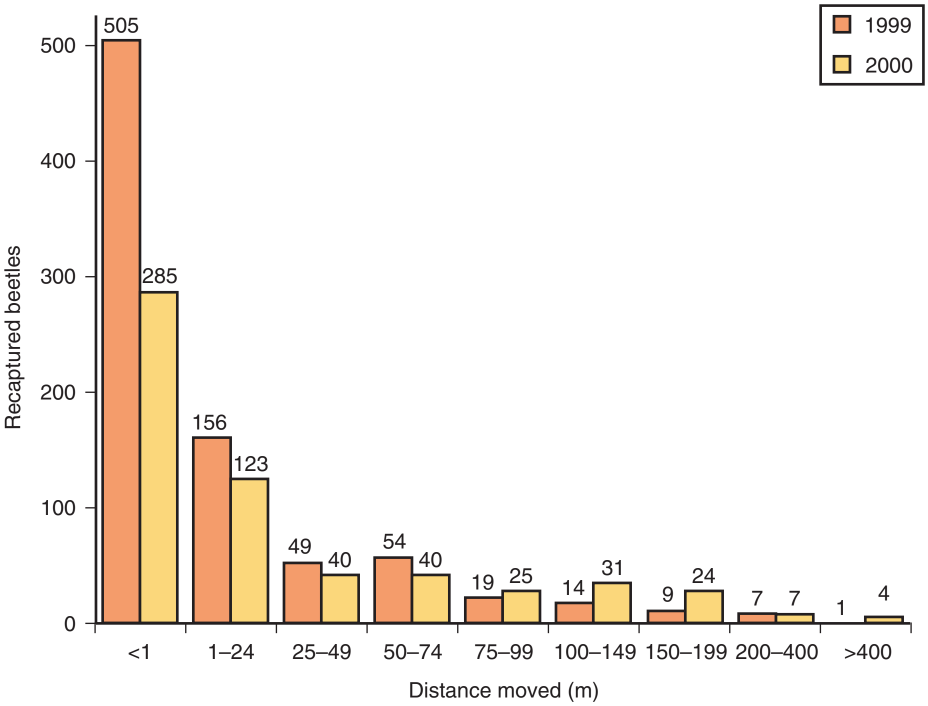


FIG. 5.5 Range of dispersal distances from a population source for the weevil, *Rhyssomatus lineaticollis*, in Iowa, United States. From St. Pierre and Hendrix (2003) with permission from the Royal Entomological Society. Please see extended permission list pg 570.

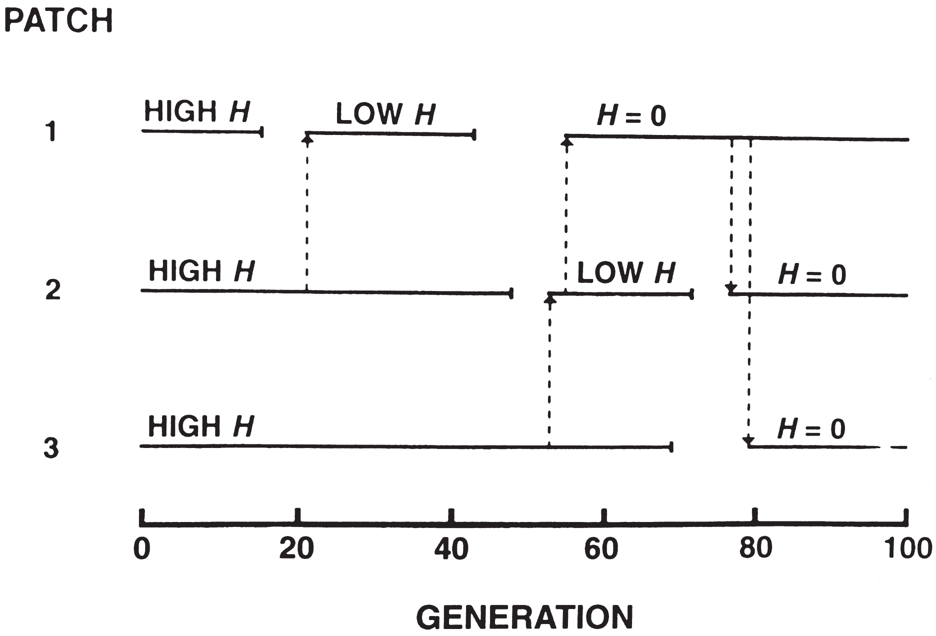


FIG. 5.6 Simulated population heterozygosity (H) over time in three habitat patches. Extinction is indicated by short vertical bars on the right end of horizontal lines; recolonization is indicated by arrows. From Hedrick and Gilpin (1998).

tive dispersal declines as the probability of encountering inhospitable patches increases.

The contribution of dispersing individuals to genetic heterogeneity in a population depends on a number of factors. The genetic heterogeneity of the source population determines the gene pool from which dispersants come. Dispersing individuals represent a proportion of the total gene pool for the population. More heterogeneous demes have greater contributions to the genetic heterogeneity of target or founded demes than do less heterogeneous demes (Fig. 5.6) (Hedrick and Gilpin 1997). The number or proportion of individuals that disperse affects their genetic heterogeneity. If certain genotypes are more likely to disperse, then the frequencies of these genotypes in the source population may decline, unless balanced by immigration. Distances between demes influence the degree of gene exchange through dispersal. Local demes will be influenced more by the genotypes of dispersants from neighboring demes than by more distant demes. Gene flow may be precluded for sufficiently fragmented populations. This is an increasing concern for demes restricted to isolated refugia. Populations consisting of small, isolated demes may be incapable of sufficient interaction to sustain viability.

III. LIFE HISTORY CHARACTERISTICS

Life history adaptation to environmental conditions usually involves complementary selection of natality and dispersal strategies. General life history strategies appear to be related to habitat stability.

MacArthur and Wilson (1967) distinguished two life history strategies related to habitat stability and importance of colonization and rapid population establishment. The r-strategy generally characterizes "weedy" species adapted to colonize and dominate new or ephemeral habitats quickly (Janzen 1977). These species are opportunists that quickly colonize new resources but are poor competitors and cannot persist when competition increases in stable habitats. By contrast, the K strategy is characterized by low rates of natality and dispersal but high investment of resources in storage and individual offspring to ensure their survival. These species are adapted to persist under stable conditions, where competition is intense, but reproduce and disperse too slowly to be good colonizers. Specific characteristics of the two strategies (Table 5.1) have been the subject of debate (Boyce 1984). For example, small size with smaller resource requirements might be favored by K selection (Boyce 1984), although larger organisms usually show more efficient resource use. Nevertheless, this model has been useful for understanding selection of life history attributes (Boyce 1984).

Insects generally are considered to exemplify the r-strategy because of their relatively short life spans, Type 3 survivorship, and rapid reproductive and dispersal rates. However, among insects, a wide range of r-K strategies have been identified. For example, low-order streams (characterized by narrow constrained channels and steep topographic gradients) experience wider variation in water flow and substrate movement, compared to higher-order streams (characterized by broader floodplains and shallower topographic gradients). Insects associated with lower-order streams tend to be more r-selected than are insects associated with slower water and greater accumulation of detritus (Reice 1985). Similarly, ephemeral terrestrial habitats are dominated by species with higher natality and dispersal rates (e.g., aphids and Collembola), compared to more stable habitats, dominated by Lepidoptera, Coleoptera, and oribatid mites (Schowalter 1985, Seastedt 1984). Many species associated with relatively stable habitats are poor

TABLE 5.1 Life history characteristics of species exemplifying the r- and K-strategies

Attribute	**Ecological Strategy**	
	r (opportunistic)	**K (equilibrium)**
Homeostatic ability	Limited	Extensive
Development time	Short	Long
Life span	Short	Long
Mortality rate	High	Low
Reproductive mode	Often asexual	Sexual
Age at first brood	Early	Late
Offspring/brood	Many	Few
Broods/lifetime	Usually one	Often several
Size of offspring	Small	Large
Parental care	None	Extensive
Dispersal ability	High	Limited
Numbers dispersing	Many	Few
Dispersal mode	Random	Oriented

dispersers and are often flightless, even wingless, indicating weak selection for escape and colonization of new habitats (St. Pierre and Hendrix 2003). Such species may be at risk if environmental change increases the frequency of disturbance.

Grime (1977) modified the r-K model by distinguishing three primary life history strategies in plants, based on their relative tolerances of disturbance, competition, and stress. Clearly, these three factors are interrelated because disturbance can affect competition and stress can increase vulnerability to disturbance. Nevertheless, this model has proved useful for distinguishing the following strategies, characterizing harsh versus frequently disturbed and infrequently disturbed habitats.

The *ruderal* strategy generally corresponds to the r-selected strategy and characterizes unstable habitats; the *competitive* strategy generally corresponds to the K strategy and characterizes relatively stable habitats. The *stress-adapted* strategy characterizes species adapted to persist in harsh environments. These species usually are adapted to conserve resources and minimize exposure to extreme conditions. Insects showing the stress-adapted strategy include those adapted to tolerate freezing in arctic ecosystems or minimize water loss in desert ecosystems (see Chapter 2).

Fielding and Brusven (1995) explored correlations between plant community correspondence to Grime's (1977) strategies and the species traits (abundance, habitat breadth, phenology, and diet breadth) of the associated grasshopper assemblages. They found that the three grasshopper species associated with the ruderal plant community had significantly wider habitat and diet breadths (generalists) and had higher densities than did grasshoppers associated with the competitive or stress-adapted plant communities (Fig. 5.7). Grasshopper assemblages also could be distinguished between the competitive and stress-adapted plant communities, but these differences were only marginally significant. Nevertheless, their study suggested that insects can be classified according to Grime's (1977) model, based on their life history adaptations to disturbance, competition, or stress.

IV. PARAMETER ESTIMATION

Whereas population structure can be measured by sampling the population, estimates of natality, mortality, and dispersal require measurement of changes through time in overall rates of birth, death, and movement. The following methods have been used to estimate these population processes (Southwood 1978).

Fecundity can be estimated by measuring the numbers of eggs in dissected females or recording the numbers of eggs laid by females caged under natural conditions. Fertility can be measured if the viability of eggs can be assessed. Natality then can be estimated from data for a large number of females. Mortality can be measured by subtracting population estimates for successive life stages, by recovering and counting dead or unhealthy individuals, or by dissecting or immunoassaying to identify parasitized individuals. Dispersal capacity can be

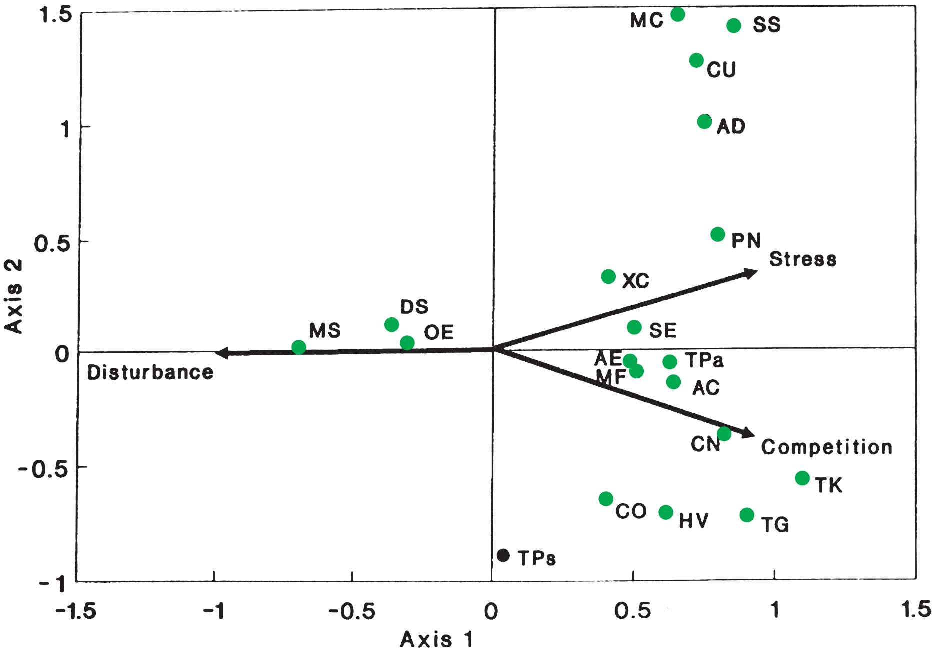


FIG. 5.7 Constrained correspondence analysis ordination of grasshopper species in southern Idaho, using Grime's (1977) classification of life history strategies based on disturbance, competition, and stress variables (*arrows*). Grasshoppers are denoted by the initials of their genus and species. The length of arrows is proportional to the influence of each variable on grasshopper species composition. Eigenvalues for axes 1 and 2 are 0.369 and 0.089, respectively. From Fielding and Brusven (1993) with permission from the Entomological Society of America.

measured in the laboratory using flight chambers to record duration of tethered flight. Natality, mortality, and dispersal also can be estimated from sequential recapture of marked individuals. However, these techniques require a number of assumptions about the constancy of natality, mortality, and dispersal and their net effects on population structure of the sample, and they do not measure natality, mortality, and dispersal directly.

Deevy (1947) was the first ecologist to apply the methods of actuaries, for determining life expectancy at a given age, to development of survival and reproduction budgets for animals. Life table analysis is the most reliable method to account for survival and reproduction of a population (Begon and Mortimer 1981, Price 1997, Southwood 1978). The advantage of this technique over others is the accounting of survival and reproduction in a way that allows for verification and comparison. For example, a change in cohort numbers at a stage when dispersal cannot occur could signal an error that requires correction or causal factors that merit examination.

Two types of life tables have been widely used by ecologists. The age-specific life table is based on the fates of individuals in a real cohort, a group of individuals born in the same time interval, whereas a time-specific life table is based on the fate of individuals in an imaginary cohort derived from the age structure of a stable population with overlapping generations at a point in time. Because most insects have discrete generations and unstable populations, the age-specific life table is more applicable than the time-specific life table.

Life tables permit accounting for the survival and reproduction of members of a cohort (Table 5.2). For simplicity, the starting size of the cohort generally is corrected to a convenient number, generally 1 or 1000 females. Females are the focus of life table budgets because of their reproductive potential. Data from many cohorts representing different birth times, population densities, and environmental conditions should be analyzed and compared to gain a broad view of natality and mortality over a wide range of conditions.

Life tables partition the life cycle into discrete time intervals or life stages (see Table 5.2). The age of females at the beginning of each period is designated by x; the proportion of females surviving at the beginning of the period, the age-specific survivorship, is designated by l_x; and the number of daughters produced by each female surviving at age x, or age-specific reproductive rate, is designated by m_x. Age-specific survivorship and reproduction can be compared between life stages to reveal patterns of mortality and reproduction. The products of per

TABLE 5.2 Examples of life tables. Note that in these examples, the same or different cohort replacement rates are obtained by the way in which per capita production of offspring is distributed among life stages.

x	l_x	m_x	l_xm_x
0	1.0	0	0
1	0.5	0	0
2	0.2	6	1.2
3	0.1	0	0
4	0	0	0
			1.2
0	1.0	0	0
1	0.5	0	0
2	0.2	0	0
3	0.1	12	1.2
4	0	0	0
			1.2
0	1.0	0	0
1	0.5	0	0
2	0.2	0	0
3	0.1	6	0.6
4	0	0	0
			0.6

x, life stage; l_x, proportion surviving at x; m_x, per capita production at x; and l_xm_x, net production at x. The sum of l_xm_x is the replacement rate, R_o.

capita production and proportion of females surviving for each stage ($l_x \cdot m_x$) can be added to yield the net production, or net replacement rate (R_0), of the cohort. Net replacement rate indicates population trend. A stable population would have $R_0 = 1$, an increasing population would have $R_0 > 1$, and a decreasing population would have $R_0 < 1$. These measurements can be used to describe population dynamics, as discussed in the next chapter.

The intensive monitoring necessary to account for survival and reproduction permits identification of factors affecting survival and reproduction. Mortality factors, as well as numbers of immigrants and emigrants, are conveniently identified and evaluated. Survivorship between cohorts can be modeled as a line with a slope of -k. This slope variable can be partitioned among factors affecting survivorship (i.e., $-k_1$, $-k_2$, $-k_3$, . . . $-k_i$). Such K-factor analysis has been used to assess the relative contributions of various factors to survival or mortality (e.g., Curry 1994, Price 1997, Varley *et al.* 1973). Factors having the greatest effect on survival and reproduction are designated *key factors* and may be useful in population management. For example, key mortality agents can be augmented for control of pest populations or mitigated for recovery of endangered species.

Measurement of insect movement and dispersal is necessary for a number of objectives (Nathan *et al.* 2003, Turchin 1998). Disappearance of individuals as a result of emigration must be distinguished from mortality for life table analysis and assessment of effective dispersal. Movement affects the probability of contact among organisms, determining their interactions. Spatial redistribution of organisms determines population structure, colonization, and metapopulation dynamics (see also Chapter 7). Several methods for measuring and modeling animal movement have been summarized by Nathan *et al.* (2003) and Turchin (1998). Most are labor intensive, especially for insects.

Effective dispersal can be reconstructed from biogeographic distributions, especially for island populations that must have been founded from mainland sources. This method does not reveal the number of dispersing individuals required for successful colonization.

Mark-recapture methods involve marking a large number of individuals and measuring their frequency in traps or observations at increasing distance from their point of release. Several methods can be used to mark individuals. Dye, stable isotope, and rare element incorporation through feeding or dusting provide markers that can be used to distinguish marked individuals from others in the recaptured sample. Some populations are self-marked by incorporation of markers unique to their birthplace or overwintering site.

Large numbers must be marked to maximize the probability of recapture at large distances. Schneider (1999) marked ca. 7,000,000 adult *Helicoverpa virescens* using internal dye, released moths at multiple sites over a 238-km^2 area, and trapped moths using pheromones at sites representing a 2000-km^2 area. Mean dispersal distances of male moths was ca. 10 km.

Leisnham and Jamieson (2002) used mark-recapture techniques to estimate immigration and emigration rates for mountain stone weta demes among large and small tors in southern New Zealand. They found that per capita immigration rate on large tors (0.019) slightly exceeded emigration rate (0.017), whereas

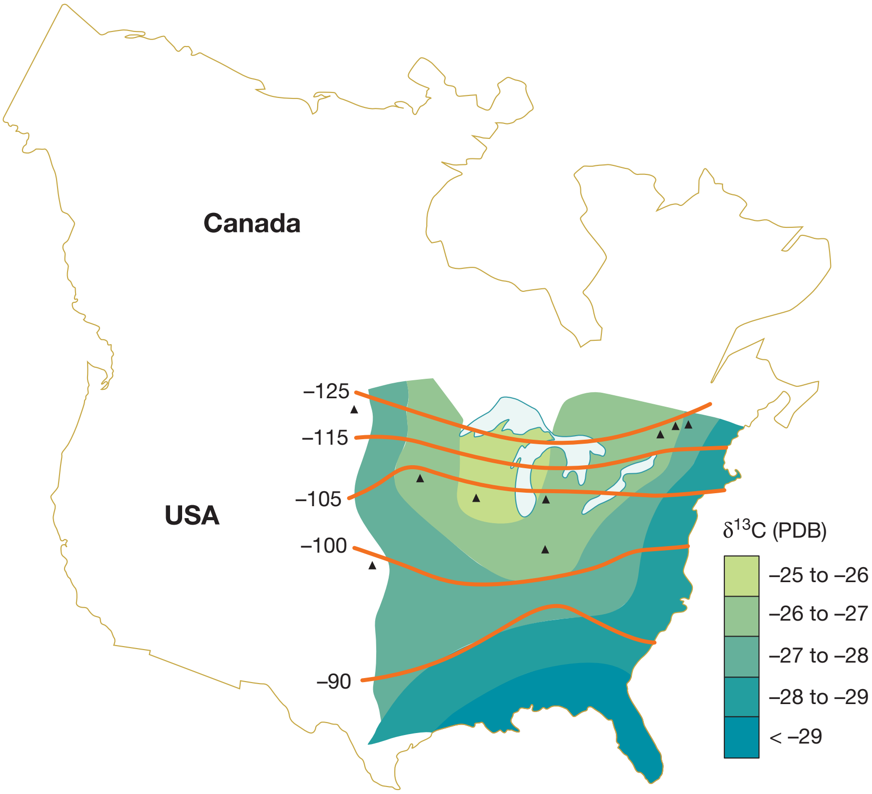


FIG. 5.8 Geographic patterns of δ^2H and δ^{13}C in wings of monarch butterflies from rearing sites (*triangles*) across the breeding range in North America. From Wassenaar and Hobson (1998) with permission from the National Academy of Sciences.

immigration rate on small tors (0.053) was lower than emigration rate (0.066), explaining the greater tendency for extinction of demes on small tors (4 of 14 over a 3-year study, compared to no extinctions among 4 large tors).

Wassenaar and Hobson (1998) used stable isotopes (^{2}H and ^{13}C) to identify the Midwestern United States as the source of most monarch butterflies, *Danaus plexippus*, overwintering at sites in Mexico (Fig. 5.8). Cronin *et al.* (2000) reported that 50% of marked checkered beetles, *Thanasimus dubius*, moved at least 1.25 km, 33% moved >2 km, and 5% dispersed >5 km, whereas 50% of their primary prey, the southern pine beetle, moved no more than 0.7 km and 95% moved no more than 2.25 km. St. Pierre and Hendrix (2003) demonstrated that 56% of recaptured weevils, *Rhyssomatus lineaticollis*, moved <1 m and 83% moved <50 m. This method can indicate the distances moved by individuals, but it does not indicate the path, which requires direct observation.

Direct observation has limited value for rapidly moving individuals, although marking individuals in various ways can enhance detection at greater distances. New technology has provided for miniaturization of radio, harmonic radar, or microwave transmitters or tags that can be used with a receiver to record the location of an individual continuously or at intervals (e.g., Riley *et al.* 1996). However, marking and electronic signaling methods could affect the behavior of tagged individuals.

New genetic techniques permit identification of the source population of dispersing individuals. However, a large number of source individuals must be genotyped to distinguish allelic frequencies of multiple sources. Dispersal frequency also may be measured in some cases by taking advantage of relationships between genetic differentiation and distance between demes.

A major challenge to future measurement of dispersal is the increasing homogenization of biotas by human-assisted invasion (e.g., Mack *et al.* 2000). A. Suarez *et al.* (2001) evaluated dispersal of Argentine ants, *Linepithema humile*, at three spatial scales—local, regional, and global—based on documented rates of spread. They discovered that these ants have two discrete dispersal modes—diffusion and jump dispersal. Local diffusion occurs at a maximum rate of 150 m yr^{-1}, whereas jump dispersal resulted in annual rates of spread of >160 km yr^{-1}, driven largely by association with humans. As species become more widespread, the source of particular populations will become more difficult to assess.

V. SUMMARY

Population systems can be described in terms of structural variables and processes that produce changes in structure. These variables indicate population status and capacity for change in response to environmental heterogeneity.

Structural variables include density, dispersion pattern of individuals and demes, age structure, sex ratio, and genetic composition. Density is the number of individuals per unit area. Dispersion is a measure of how populations are distributed in space. Regular dispersion occurs when organisms are spaced evenly among habitat or sampling units. Aggregated dispersion occurs when individuals are found in groups, for mating, for mutual defense or resource exploitation, or because of the distribution of resources. Random dispersion occurs when the locations of organisms are independent of the locations of others. Metapopulation structure describes the distribution and interaction among relatively distinct subpopulations, or demes, occurring among habitable patches over a landscape. The degree of isolation of demes influences gene flow among demes and ability to colonize or recolonize vacant patches. Age structure represents the proportion of individuals in each age class and may indicate survivorship patterns or direction of change in population size. Sex ratio is the proportion of males in the population and indicates the importance of sexual reproduction, mating system, and capacity for reproduction. Genetic composition is described by the frequencies of various alleles in the population and reflects population capacity to adapt to environmental change. Some insect populations have been shown to change gene frequencies within relatively short times in response to strong directional selection as a result of short generation times and high reproductive rates. This capacity for rapid change in gene frequencies makes insects especially capable of adapting to anthropogenic changes in environmental conditions.

Processes that produce change in population structure include natality, mortality, and dispersal. Natality is birth rate and represents the integration of individual fecundity and fertility. Natality is affected by abundance and nutritional quality of food resources, abundance and suitability of oviposition sites, availability of males, and population density. Mortality is death rate and reflects the influence of various mortality agents, including extreme weather conditions, food quality, competition, and predation. Generally, predation has a greater effect at low to moderate densities, whereas competition has a greater effect at high densities. Survivorship curves indicate three types of survivorship, based on whether mortality is consistent or concentrated near the beginning or end of the life span. Dispersal is the movement of individuals from a source and is a key to genetic mixing and colonization of vacant patches. Individuals colonizing vacant patches have a considerable influence on the genetic composition and development of the deme.

Life history strategies reflect the integration of natality, mortality, and dispersal strategies selected by habitat stability. Two life history classifications have been widely used. Both reflect the importance of disturbance and environmental stress on evolution of complementary strategies for reproduction and dispersal in harsh, stable, or unstable habitats.

Whereas population structure can be described readily by sampling the population, measurement of population processes is more difficult and requires accounting for the fate of individuals. Life table analysis is the most reliable method to account for age-specific survival and reproduction by members of a cohort. The net production of offspring by the cohort is designated the replacement rate and indicates population trend. Advances in technology are creating new opportunities to explore patterns and efficiency of long-distance dispersal. Changes in these variables and processes are the basis for population dynamics. Regulatory factors and models of population change in time and space are described in the next two chapters.

6

Population Dynamics

POPULATIONS OF INSECTS CAN CHANGE DRAMATICALLY IN SIZE OVER relatively short periods of time as a result of changes in natality, mortality, immigration, and emigration. Under favorable environmental conditions, some species have the capacity to increase population size by orders of magnitude in a few years, given their short generation times and high reproductive rates. Under adverse conditions, populations can virtually disappear for long time periods. This capacity for significant and measurable change in population size makes insects potentially useful indicators of environmental change, often serious "pests" affecting human activities, and important engineers of ecosystem properties that also may affect global conditions. The role of insects as pests has provided the motivation for an enormous amount of research to identify factors affecting insect population dynamics; to develop models to predict population change; and, more recently, to evaluate effects of insect populations on ecosystem properties. Consequently, methods and models for describing population change are most developed for economically important insects.

Predicting the effects of global change has become a major goal of research on population dynamics. Insect populations respond to changes in habitat conditions and resource quality (Heliövaara and Väisänen 1993, Lincoln *et al*. 1993; see Chapter 2). Their responses to current environmental changes help us to anticipate responses to future environmental changes. Disturbances, in particular, influence population systems abruptly, but these effects are integrated by changes in natality, mortality, and dispersal rates. Factors that normally regulate population size, such as resource availability and predation, also are affected by disturbance. As a result, population regulation may be disrupted by disturbance for some insect species. Models of population change generally do not incorporate effects of disturbance. This chapter addresses temporal patterns of abundance, factors causing or regulating population fluctuation, and models of population dynamics.

I. POPULATION FLUCTUATION

Insect populations can fluctuate dramatically over time. If environmental conditions change in a way that favors insect population growth, the population will increase until regulatory factors reduce and finally stop population growth rate. Some populations can vary in density as much as 10^5-fold (Mason 1996, Mason and Luck 1978, Royama 1984, Schell and Lockwood 1997), but most populations vary less than this (Berryman 1981, D. Strong *et al*. 1984). The amplitude and frequency of population fluctuations can be used to describe three general patterns. Stable populations fluctuate relatively little over time, whereas irruptive and cyclic populations show wide fluctuations.

Irruptive populations sporadically increase to peak numbers followed by a decline. Certain combinations of life history traits may be conducive to irruptive fluctuation. Larsson *et al*. (1993) and Nothnagle and Schultz (1987) reported that comparison of irruptive and nonirruptive species of sawflies and Lepidoptera from European and North American forests indicated differences in attributes between these two groups. Irruptive species generally are controlled by only one or a few factors, whereas populations of nonirruptive species are controlled by many factors. In addition, irruptive Lepidoptera and sawfly species tend to be gregarious, have a single generation per year, and are sensitive to changes in quality or availability of their particular resources, whereas nonirruptive species do not share this combination of traits.

Cyclic populations oscillate at regular intervals. Cyclic patterns of population fluctuation have generated the greatest interest among ecologists. Cyclic patterns can be seen over different time scales and may reflect a variety of interacting factors.

Strongly seasonal cycles of abundance can be seen for multivoltine species such as aphids and mosquitoes. Aphid population size is correlated with periods of active nutrient translocation by host plants (Dixon 1985). Hence, populations of most species peak in the spring when nutrients are being translocated to new growth, and populations of many species (especially those feeding on deciduous hosts) peak again in the fall when nutrients are being resorbed from senescing foliage. This pattern can be altered by disturbance. Schowalter and Crossley (1988) reported that sustained growth of early successional vegetation following clearcutting of a deciduous forest supported continuous growth of aphid populations during the summer (Fig. 6.1). Seven dominant mosquito species in Florida during 1998–2000 showed peak abundances at different times of the year, but the interannual pattern varied as a result of particular environmental conditions, including flooding (Zhong *et al*. 2003).

Longer-term cycles are apparent for many species. Several forest Lepidoptera exhibit cycles with periods of ca. 10 years, 20 years, 30 years, or 40 years (Berryman 1981, Mason and Luck 1978, Price 1997, Royama 1992, Swetnam and Lynch 1993) or combinations of cycles (Speer *et al*. 2001). For example, spruce budworm,

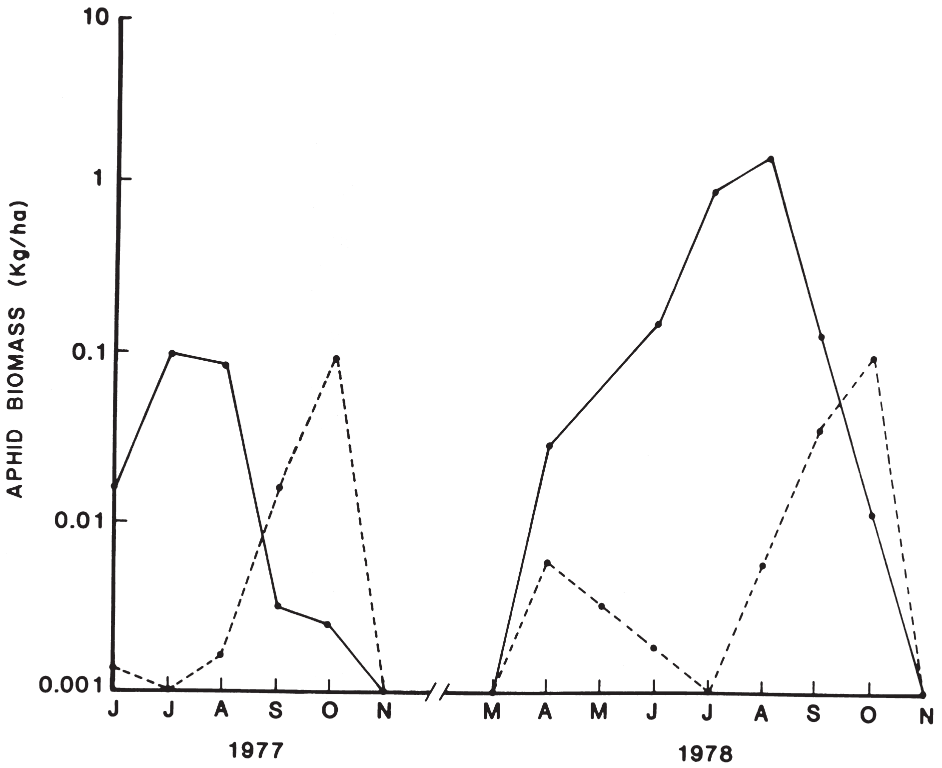


FIG. 6.1 Seasonal trends in aphid biomass in an undisturbed (*dotted line*) and an early successional (*solid line*) mixed-hardwood forest in North Carolina. The early successional forest was clearcut in 1976–1977. Peak abundances in spring and fall on the undisturbed watershed reflect nutrient translocation during periods of foliage growth and senescence; continued aphid population growth during the summer on the disturbed watershed reflects the continued production of foliage by regenerating plants. From Schowalter (1985).

Choristoneura fumiferana, populations have peaked at approximately 25–30-year intervals over a 250-year period in eastern North America (Fig. 6.2), whereas Pandora moth, *Coloradia pandora*, populations have shown a combination of 20- and 40-year cycles over a 622-year period in western North America (Fig. 6.3). In many cases, population cycles are synchronized over large areas, suggesting the influence of a common widespread trigger such as climate, sunspot, lunar, or ozone cycles (W. Clark 1979, Price 1997, Royama 1984, 1992, Speer *et al.* 2003). Alternatively, P. Moran (1953) suggested, and Royama (1992) demonstrated (using models), that synchronized cycles could result from correlations among controlling factors. Hence, the cause of synchrony can be independent of the cause of the cyclic pattern of fluctuation. Generally, peak abundances are maintained only for a few (2–3) years, followed by relatively precipitous declines (see Figs. 6.2 and 6.3).

Explanations for cyclic population dynamics include climatic cycles and changes in insect gene frequencies or behavior, food quality, or susceptibility to

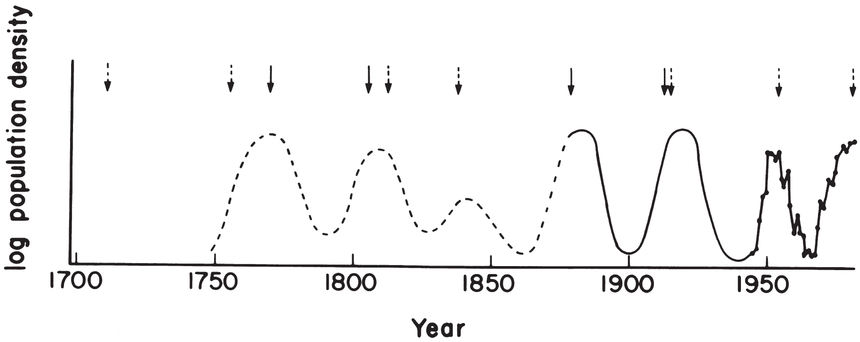


FIG. 6.2 Spruce budworm population cycles in New Brunswick and Quebec over the past 200 years, from sampling data since 1945, from historical records between 1978 and 1945, and from radial growth-ring analysis of surviving trees prior to 1878. Arrows indicate the years of first evidence of reduced ring growth. Data since 1945 fit the log scale, but the amplitude of cycles prior to 1945 are arbitrary. From Royama (1984) with permission from the Ecological Society of America.

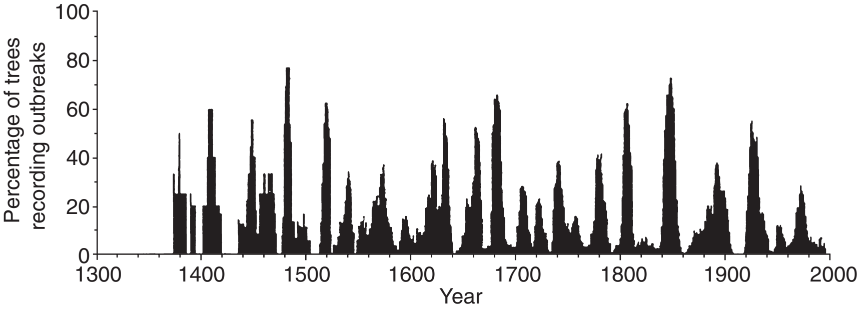


FIG. 6.3 Percentage of ponderosa pine trees recording outbreaks of pandora moth in old-growth stands in central Oregon, United States. From Speer *et al.* (2001) with permission from the Ecological Society of America. Please see extended permission list pg 570.

disease that occur during large changes in insect abundance (J. Myers 1988). Climatic cycles may trigger insect population cycles directly through changes in mortality or indirectly through changes in host condition or susceptibility to pathogens. Changes in gene frequencies or behavior may permit rapid population growth during a period of reduced selection. In particular, reduced selection under conditions favorable for rapid population growth may permit increased frequencies of deleterious alleles that become targets of intense negative selection when conditions become less favorable. Depletion of food resources during an outbreak may impose a time lag for recovery of depleted resources to levels capable of sustaining renewed population growth (e.g., W. Clark 1979). Epizootics of entomopathogens may occur only above threshold densities. Sparse populations near their extinction threshold (see the next section) may require several years to recover sufficient numbers for rapid population growth. Berryman (1996), Royama (1992), and Turchin (1990) have demonstrated the importance of delayed effects (time lags) of regulatory factors (especially predation or parasitism) to the generation of cyclic pattern.

Changes in population size can be described by four distinct phases (Mason and Luck 1978). The *endemic phase* is the low population level maintained between outbreaks. The beginning of an outbreak cycle is triggered by a disturbance or other environmental change that allows the population to increase in size above its *release threshold.* This threshold represents a population size at which reproductive momentum results in escape of at least a portion of the population from normal regulatory factors, such as predation. Despite the importance of this threshold to population outbreaks, few studies have established its size for any insect species. Schowalter *et al*. (1981b) reported that local outbreaks of southern pine beetle, *Dendroctonus frontalis*, occurred when demes reached a critical size of about 100,000 beetles by early June. Above the release threshold, survival is relatively high and population growth continues uncontrolled during the *release phase.* During this period, emigration peaks and the population spreads to other suitable habitat patches (see Chapter 7). Resources eventually become limiting, as a result of depletion by the growing population, and predators and pathogens respond to increased prey or host density and stress. Population growth slows and abundance reaches a *peak.* Competition, predation, and pathogen epizootics initiate and accelerate population *decline.* Intraspecific competition and predation rates then decline as the population reenters the endemic phase.

Outbreaks of some insect populations have become more frequent and intense in crop systems or natural monocultures where food resources are relatively unlimited or where manipulation of disturbance frequency has created favorable conditions (e.g., Kareiva 1983, Wickman 1992). In other cases, the frequency of recent outbreaks has remained within ranges for frequencies of historic outbreaks, but the extent or severity has increased as a result of anthropogenic changes in vegetation structure or disturbance regime (Speer *et al*. 2001). However, populations of many species fluctuate at amplitudes that are insufficient to cause economic damage and, therefore, do not attract attention. Some of these species may experience more conspicuous outbreaks under changing environmental conditions (e.g., introduction into new habitats or large-scale conversion of natural ecosystems to managed ecosystems).

II. FACTORS AFFECTING POPULATION SIZE

Populations are affected by a variety of intrinsic and extrinsic factors. Intrinsic factors include intraspecific competition, cannibalism, territoriality, etc. Extrinsic factors include abiotic conditions and other species. Populations showing wide amplitude of fluctuation may have weak intrinsic ability to regulate population growth (e.g., through depressed natality in response to crowding). Rather, such populations may be regulated by available food supply, predation, or other extrinsic factors. These factors can influence population size in two primary ways. If the proportion of organisms affected by a factor is constant for any population density, or the effect of the factor does not depend on population density, the factor is considered to have a *density-independent* effect. Conversely, if the proportion of organisms affected varies with density, or the effect of the factor depends on population density, then the factor is considered to have a *density-dependent* effect (Begon and Mortimer 1981, Berryman 1981, L. Clark *et al*. 1967, Price 1997).

The distinction between density independence and density dependence is often confused for various reasons. First, many factors may act in both density-independent and density-dependent manners, depending on circumstances. For example, climatic factors or disturbances often are thought to affect populations in a density-independent manner because the same proportion of exposed individuals usually is affected at any population density. However, if shelter from unfavorable conditions is limited, the proportion of individuals exposed (and, therefore, the effect of the climatic factor or disturbance) may be related to population density. Furthermore, a particular factor may have a density-independent effect over one range of population densities and a density-dependent effect over another range of densities. A plant defense may have a density-independent effect until herbivore densities reach a level that triggers induced defenses. Generally, population size is modified by abiotic factors, such as climate and disturbance, but maintained near an equilibrium level by density-dependent biotic factors.

A. Density-Independent Factors

Insect populations are highly sensitive to changes in abiotic conditions, such as temperature, water availability, etc., which affect insect growth and survival (see Chapter 2). Changes in population size of some insects have been related directly to changes in climate or to disturbances (e.g., Greenbank 1963, Kozár 1991, Porter and Redak 1996, Reice 1985). In some cases, climate fluctuation or disturbance affects resource values for insects. For example, loss of riparian habitat as a result of agricultural practices in western North America may have led to extinction of the historically important Rocky Mountain grasshopper, *Melanoplus spretus* (Lockwood and DeBrey 1990).

Many environmental changes occur relatively slowly and cause gradual changes in insect populations as a result of subtle shifts in genetic structure and individual fitness. Other environmental changes occur more abruptly and may trigger rapid change in population size because of sudden changes in natality, mortality, or dispersal.

Disturbances are particularly important triggers for inducing population change because of their acute disruption of population structure and of resource, substrate, and other ecosystem conditions. The disruption of population structure can alter community structure and cause changes in physical, chemical, and biological conditions of the ecosystem. Disturbances can promote or truncate population growth, depending on species tolerances to particular disturbance or postdisturbance conditions.

Some species are more tolerant of particular disturbances, based on adaptation to regular recurrence. For example, plants in fire-prone ecosystems tend to have attributes that protect meristematic tissues, whereas those in frequently flooded ecosystems can tolerate root anaerobiosis. Generally, insects do not have specific adaptations to survive disturbance, given their short generation times relative to disturbance intervals, and unprotected populations may be greatly reduced. Species that do show some disturbance-adapted traits, such as orientation to smoke plumes or avoidance of litter accumulations in fire-prone ecosystems (W. Evans 1966, K. Miller and Wagner 1984), generally have longer (2–5-year) generation times that would increase the frequency of generations experiencing a disturbance. Most species are affected by postdisturbance conditions. Disturbances affect insect populations both directly and indirectly.

Disturbances create lethal conditions for many insects. For example, fire can burn exposed insects (Porter and Redak 1996, P. Shaw *et al*. 1987) or raise temperatures to lethal levels in unburned microsites. Tumbling cobbles in flooding streams can crush benthic insects (Reice 1985). Flooding of terrestrial habitats can create anaerobic soil conditions. Drought can raise air and soil temperatures and cause desiccation (Mattson and Haack 1987). Populations of many species can suffer severe mortality as a result of these factors, and rare species may be eliminated (P. Shaw *et al*. 1987, Schowalter 1985). Willig and Camilo (1991) reported the virtual disappearance of two species of walkingsticks, *Lamponius portoricensis* and *Agamemnon iphimedeia*, from tabonuco, *Dacryodes excelsa*, forests in Puerto Rico following Hurricane Hugo. Drought can reduce water levels in aquatic ecosystems, reducing or eliminating habitat for some aquatic insects. In contrast, storms may redistribute insects picked up by high winds. Torres (1988) reviewed cases of large numbers of insects being transported into new areas by hurricane winds, including swarms of African desert locusts, *Schistocerca gregaria,* deposited on Caribbean islands.

Mortality depends on disturbance intensity and scale and species adaptation. K. Miller and Wagner (1984) reported that the pandora moth preferentially pupates on soil with sparse litter cover, under open canopy, where it is more likely to survive frequent understory fires. This habit would not protect pupae during more severe fires. Small-scale disturbances affect a smaller proportion of the population than do larger-scale disturbances. Large-scale disturbances, such as volcanic eruptions or hurricanes, could drastically reduce populations over much of the species range, making such populations vulnerable to extinction. The potential for disturbances to eliminate small populations or critical local demes of fragmented metapopulations has become a serious obstacle to restoration of endangered (or other) species (P. Foley 1997).

Disturbances indirectly affect insect populations by altering the postdisturbance environment. Disturbance affects abundance or physiological condition of hosts and abundances or activity of other associated organisms (Mattson and Haack 1987, T. Paine and Baker 1993). Selective mortality to disturbance-intolerant plant species reduces the availability of a resource for associated herbivores. Similarly, long disturbance-free intervals can lead to eventual replacement of ruderal plant species and their associated insects. Changes in canopy cover or plant density alter vertical and horizontal gradients in light, temperature, and moisture that influence habitat suitability for insect species; alter plant conditions, including nitrogen concentrations; and can alter vapor diffusion patterns that influence chemoorientation by insects (Cardé 1996, Kolb *et al*. 1998, Mattson and Haack 1987, J. Stone *et al*. 1999).

Disturbances injure or stress surviving hosts or change plant species density or apparency. The grasshopper, *Melanoplus differentialis*, prefers wilted foliage of sunflower to turgid foliage (A. Lewis 1979). Fire or storms can wound surviving plants and increase their susceptibility to herbivorous insects. Lightning-struck (Fig. 6.4) or windthrown trees are particular targets for many bark beetles

FIG. 6.4 Lightning strike or other injury impairs tree defense systems. Injured, diseased, or stressed trees usually are targets of bark beetle colonization.

and provide refuges for these insects at low population levels (Flamm *et al.* 1993, T. Paine and Baker 1993). Drought stress can cause audible cell-wall cavitation that may attract insects adapted to exploit water-stressed hosts (Mattson and Haack 1987). Stressed plants may alter their production of particular amino acids or suppress production of defensive chemicals to meet more immediate metabolic needs, thereby affecting their suitability for particular herbivores (Haglund 1980, Lorio 1993, R. Waring and Pitman 1983). If drought or other disturbances stress large numbers of plants surrounding these refuges, small populations can reach epidemic sizes quickly (Mattson and Haack 1987). Plant crowding, as a result of planting or long disturbance-free intervals, causes competitive stress. High densities or apparencies of particular plant species facilitate host colonization and population growth, frequently triggering outbreaks of herbivorous species (Mattson and Haack 1987).

Changes in abundances of competitors, predators, and pathogens also affect postdisturbance insect populations. For example, phytopathogenic fungi establishing in, and spreading from, woody debris following fire, windthrow, or harvest can stress infected survivors and increase their susceptibility to bark beetles and other wood-boring insects (T. Paine and Baker 1993). Drought or solar exposure resulting from disturbance can reduce the abundance or virulence of entomopathogenic fungi, bacteria, or viruses (Mattson and Haack 1987, Roland and Kaupp 1995). Disturbance or fragmentation reduce the abundances and activity of some predators and parasites (Kruess and Tscharntke 1994, Roland and Taylor 1997) and may induce or support outbreaks of defoliators (Roland 1993). Alternatively, fragmentation can interrupt spread of some insect populations by creating inhospitable barriers (Schowalter *et al.* 1981b).

Population responses to direct or indirect effects vary, depending on scale of disturbance (see Chapter 7). Few natural experiments have addressed the effects of scale. Clearly, a larger-scale event should affect environmental conditions and populations within the disturbed area more than would a smaller-scale event. Shure and Phillips (1991) compared arthropod abundances in clearcuts of different sizes in the southeastern United States (Fig. 6.5). They suggested that the greater differences in arthropod densities in larger clearcuts reflected the steepness of environmental gradients from the clearcut into the surrounding forest. The surrounding forest has a greater effect on environmental conditions within a small canopy opening than within a larger opening.

The capacity for insect populations to respond quickly to abrupt changes in environmental conditions (disturbances) indicates their capacity to respond to more gradual environmental changes. Insect outbreaks have become particularly frequent and severe in landscapes that have been significantly altered by human activity (K. Hadley and Veblen 1993, Huettl and Mueller-Dombois 1993, Wickman 1992). Anthropogenic suppression of fire; channelization and clearing of riparian areas; and conversion of natural, diverse vegetation to rapidly growing, commercially valuable crop species on a regional scale have resulted in more severe disturbances and dense monocultures of susceptible species that support widespread outbreaks of adapted insects (e.g., Schowalter and Lowman 1999).

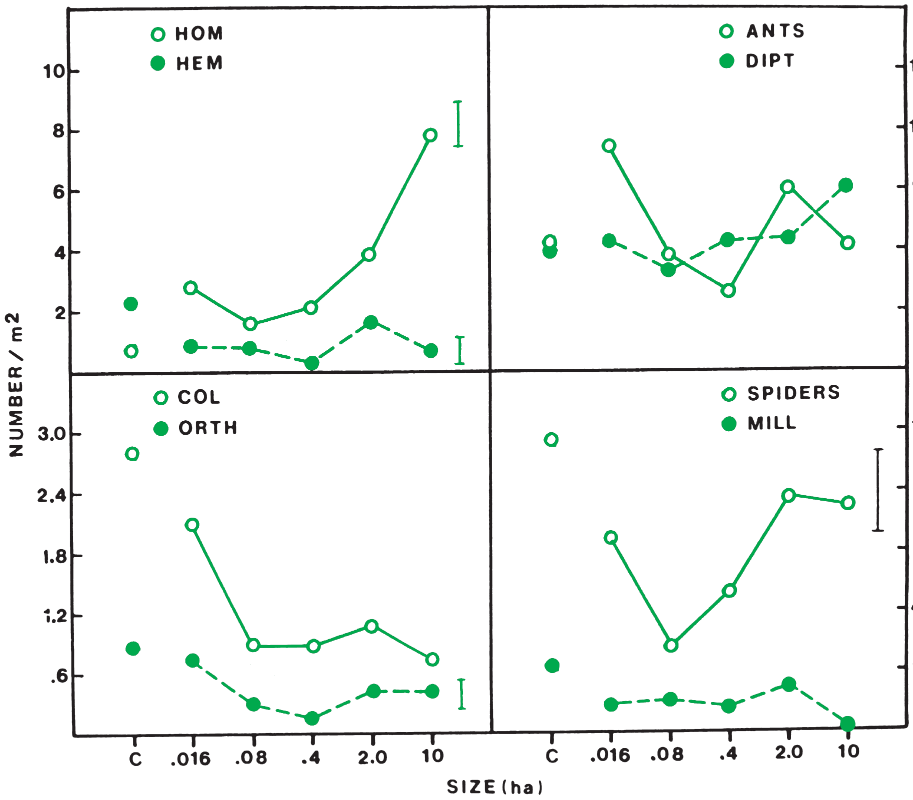


FIG. 6.5 Densities of arthropod groups during the first growing season in uncut forest (*C*) and clearcut patches ranging in size from 0.016 ha to 10 ha. For groups showing significant differences between patch sizes, vertical bars indicate the least significant difference ($P < 0.05$). HOM, Homoptera; HEM, Hemiptera; COL, Coleoptera; ORTH, Orthoptera; DIPT, Diptera; and MILL, millipedes. From Shure and Phillips (1991) with permission from Springer-Verlag. Please see extended permission list pg 570.

Insect populations also are likely to respond to changing global temperature, precipitation patterns, atmospheric and water pollution, and atmospheric concentrations of CO_2 and other trace gases (e.g., Alstad *et al.* 1982, Franklin *et al.* 1992, Heliövaara 1986, Heliövaara and Väisänen 1993, Hughes and Bazzaz 1997, Lincoln *et al.* 1993, Marks and Lincoln 1996, D. Williams and Liebhold 2002). Grasshopper populations are favored by warm, dry conditions (Capinera 1987), predicted by climate change models to increase in many regions. D. Williams and Liebhold (2002) projected increased outbreak area and shift northward for southern pine beetle, *Dendroctonus frontalis*, but reduced outbreak area and shift to higher elevations for the mountain pine beetle, *D. ponderosae*, in North America as a result of increasing temperature. Interaction among multiple factors changing simultaneously may affect insects differently than predicted from responses to individual factors (e.g., Franklin *et al.* 1992, Marks and Lincoln 1996).

The similarity in insect population responses to natural versus anthropogenic changes in the environment depends on the degree to which anthropogenic changes create conditions similar to those created by natural changes. For example, natural disturbances usually remove less biomass from a site than do harvest or livestock grazing. This difference likely affects insects that depend on postdisturbance biomass, such as large woody debris, either as a food resource or refuge from exposure to altered temperature and moisture (Seastedt and Crossley 1981a). Anthropogenic disturbances leave straighter and more distinct boundaries between disturbed and undisturbed patches (because of ownership or management boundaries), affecting the character of edges and the steepness of environmental gradients into undisturbed patches (J. Chen *et al*. 1995, Roland and Kaupp 1995). Similarly, the scale, frequency, and intensity of prescribed fires may differ from natural fire regimes. In northern Australia, natural ignition would come from lightning during storm events at the onset of monsoon rains, whereas prescribed fires often are set during drier periods to maximize fuel reduction (Braithwaite and Estbergs 1985). Consequently, prescribed fires burn hotter, are more homogeneous in their severity, and cover larger areas than do lower-intensity, more patchy fires burning during cooler, moister periods.

Few studies have evaluated the responses of insect populations to changes in multiple factors. For example, habitat fragmentation, climate change, acid precipitation, and introduction of exotic species may influence insect populations interactively in many areas. For example, stepwise multiple regression indicated that persistence of native ant species in coastal scrub habitats in southern California was best predicted by the abundance of invasive Argentine ants, *Linepithema humile*; size of habitat fragments; and time since fragment isolation (A. Suarez *et al*. 1998).

B. Density-Dependent Factors

Primary density-dependent factors include intraspecific and interspecific competition, for limited resources, and predation. The relative importance of these factors has been the topic of much debate. Malthus (1789) wrote the first theoretical treatise describing the increasing struggle for limited resources by growing populations. Effects of intraspecific competition on natality, mortality, and dispersal have been demonstrated widely (see Chapter 5). As competition for finite resources becomes intense, fewer individuals obtain sufficient resources to survive, reproduce, or disperse. Similarly, a rich literature on predator–prey interactions generally, and biocontrol agents in particular, has shown the important density-dependent effects of predators, parasitoids, parasites, and pathogens on prey populations (e.g., Carpenter *et al*. 1985, Marquis and Whelan 1994, Parry *et al*. 1997, Price 1997, Tinbergen 1960, van den Bosch *et al*. 1982, Van Driesche and Bellows 1996). Predation rates usually increase as prey abundance increases, up to a point at which predators become satiated. Predators respond both behaviorally and numerically to changes in prey density (see Chapter 8). Predators can be attracted to an area of high prey abundance, a behavioral response, and increase production of offspring as food supply increases, a numeric response.

Cooperative interactions among individuals lead to inverse density dependence. Mating success (and thus natality) increases as density increases. Some insects show increased ability to exploit resources as density increases. Examples include bark beetles that must aggregate to kill trees, a necessary prelude to successful reproduction (Berryman 1997, Coulson 1979), and social insects that increase thermoregulation and recruitment of nestmates to harvest suitable resources as colony size increases (Heinrich 1979, Matthews and Matthews 1978).

Factors affecting population size can operate over a range of time delays. For example, fire affects numbers immediately (no time lag) by killing exposed individuals, whereas predation requires some period of time (time lag) for predators to aggregate in an area of dense prey and to produce offspring. Hence, increased prey density is followed by increased predator density only after some time lag. Similarly, as prey abundance decreases, predators disperse or cease reproduction, but only after a time lag.

C. Regulatory Mechanisms

When population size exceeds the number of individuals that can be supported by existing resources, competition and other factors reduce population size until it reaches levels in balance with resource supply. This equilibrium population size, which can be sustained indefinitely by resource availability, is termed the *carrying capacity* of the environment and is designated as *K*. Carrying capacity is not constant; it depends on factors that affect both the abundance and suitability of necessary resources, including the intensity of competition with other species that also use those particular resources.

Density-independent factors modify population size, but only density-dependent factors can regulate population size, in the sense of stabilizing abundance near carrying capacity. Regulation requires environmental feedback, such as through density-dependent mechanisms that reduce population growth at high densities but allow population growth at low densities (Isaev and Khlebopros 1979). Nicholson (1933, 1954a, b, 1958) first postulated that density-dependent biotic interactions are the primary factors determining population size. Andrewartha and Birch (1954) challenged this view, suggesting that density-dependent processes generally are of minor importance in determining abundance. This debate was resolved with recognition that regulation of population size requires density-dependent processes, but abundance is determined by all factors that affect the population (Begon and Mortimer 1981, Isaev and Khlebopros 1979). However, debate continues over the relative importances of competition and predation, the so-called "bottom-up" (or resource concentration/limitation) and "top-down" (or "trophic cascade") hypotheses, for regulating population sizes (see also Chapter 9).

Bottom-up regulation is accomplished through the dependence of populations on resource supply. Suitable food is most often invoked as the limiting resource, but suitable shelter and oviposition sites also may be limiting. As populations grow, these resources become the objects of intense competition, reducing natality and increasing mortality and dispersal (see Chapter 5), and eventually reducing population growth. As population size declines, resources become relatively more available and support population growth. Hence, a population should tend to fluctuate around the size (carrying capacity) that can be sustained by resource supply.

Top-down regulation is accomplished through the response of predators and parasites to increasing host population size. As prey abundance increases, predators and parasites encounter more prey. Predators respond functionally to increased abundance of a prey species by learning to acquire prey more efficiently and respond numerically by increasing population size as food supply increases. Increased intensity of predation reduces prey numbers. Reduced prey availability limits food supply for predators and reduces the intensity of predation. Hence a prey population should fluctuate around the size determined by intensity of predation.

A number of experiments have demonstrated the dependence of insect population growth on resource availability, especially the abundance of suitable food resources (e.g., M. Brown *et al*. 1987, Cappuccino 1992, Harrison 1994, Lunderstädt 1981, Ohgushi and Sawada 1985, Polis and Strong 1996, Price 1997, Ritchie 2000, Schowalter and Turchin 1993, Schultz 1988, Scriber and Slansky 1981, Varley and Gradwell 1970). For example, Schowalter and Turchin (1993) demonstrated that growth of southern pine beetle populations, measured as number of host trees killed, was significant only under conditions of high host density and low nonhost density (Fig. 6.6). However, some populations appear not to be food limited (Wise 1975). Many exotic herbivores are generalists that are regulated poorly in the absence of coevolved predators, although this also could reflect poor defensive capacity by nonadapted plants.

Population regulation by predators has been supported by experiments demonstrating population growth following predator removal (Carpenter and Kitchell 1987, 1988, Dial and Roughgarden 1995, Marquis and Whelan 1994, Oksanen 1983). Manipulations in multiple-trophic–level systems have shown that a manipulated increase at one predator trophic level causes reduced abundance of the next lower trophic level and increased abundance at the second trophic level down (Carpenter and Kitchell 1987, 1988, Letourneau and Dyer 1998). However, in many cases, predators appear simply to respond to prey abundance without regulating prey populations (Parry *et al*. 1997), and the effect of predation and parasitism often is delayed and hence less obvious than the effects of resource supply.

Regulation by lateral factors does not involve other trophic levels. Interference competition, territoriality, cannibalism, and density-dependent dispersal have been considered to be lateral factors that may have a primary regulatory role (Harrison and Cappuccino 1995). For example, Fox (1975a) reviewed studies indicating that cannibalism is a predictable part of the life history of some species, acting as a population control mechanism that rapidly decreases the number of competitors, regardless of food supply. In the backswimmer, *Notonecta hoffmanni*, cannibalism of young nymphs by older nymphs occurred even when alter-

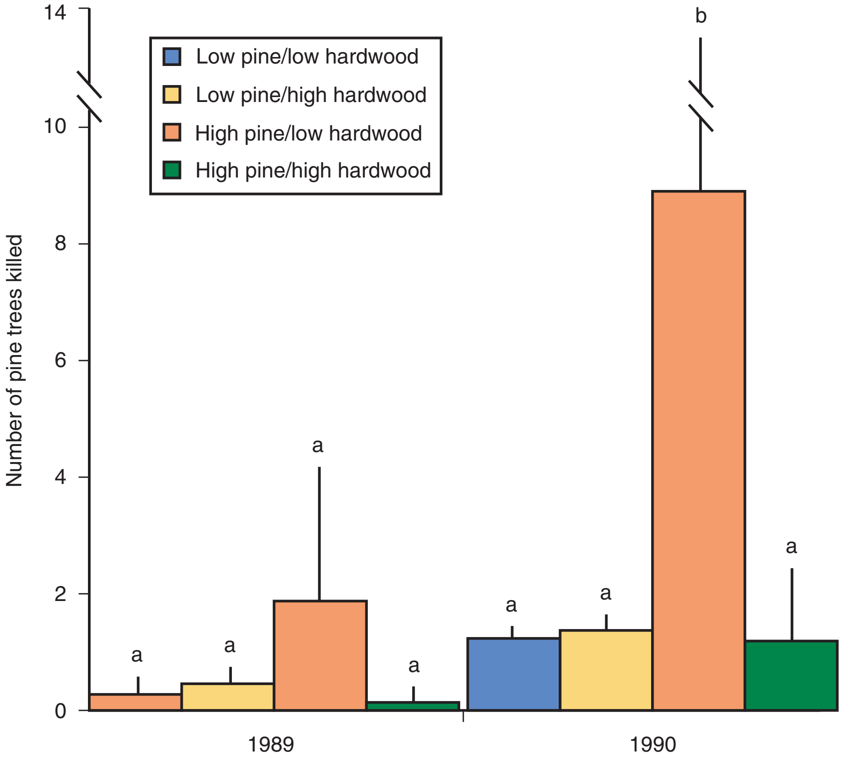


FIG. 6.6 Effect of host (pine) and nonhost (hardwood) densities on population growth of the southern pine beetle, measured as pine mortality in 1989 (Mississippi) and 1990 (Louisiana). Low pine = 11–14 m^2 ha^{-1} basal area; high pine = 23–29 m^2 ha^{-1} basal area; low hardwood = 0–4 m^2 ha^{-1} basal area; high hardwood = 9–14 m^2 ha^{-1} basal area. Vertical lines indicate standard error of the mean. Bars under the same letter did not differ at an experimentwise error rate of $P < 0.05$ for data combined for the 2 years. Data from Schowalter and Turchin (1993).

native prey were abundant (Fox 1975b). In other species, any exposed or unprotected individuals are attacked (Fox 1975a). However, competition clearly is affected by resource supply.

All populations probably are regulated simultaneously by bottom-up, top-down, and lateral factors. Some resources are more limiting than others for all species, but changing environmental conditions can affect the abundance or suitability of particular resources and directly or indirectly affect higher trophic levels (M. Hunter and Price 1992, Polis and Strong 1996, Power 1992). For example, environmental changes that stress vegetation can increase the suitability of a food plant without changing its abundance. Under such circumstances, the disruption of bottom-up regulation results in increased prey availability, and perhaps suitability (Stamp 1992, Traugott and Stamp 1996), for predators and parasites, resulting in increased abundance at that trophic level. Species often respond differentially to the same change in resources or predators. Ritchie (2000) reported that experimental fertilization (with nitrogen) of grassland plots resulted in increased non-grass quality for, and density of, polyphagous grasshoppers but did not affect grass quality and reduced density of grass-feeding grasshoppers. Density-dependent competition and dispersal, as well as increased predation, eventually cause population decline to levels at which these regulatory factors become less operative.

Harrison and Cappuccino (1995) compiled data from 60 studies in which bottom-up, top-down, or lateral density-dependent regulatory mechanisms were evaluated for populations of invertebrates, herbivorous insects, and vertebrates. They reported that bottom-up regulation was apparent in 89% of the studies, overall, compared to observation of top-down regulation in 39% and lateral regulation in 79% of the studies.

Top-down regulation was observed more frequently than bottom-up regulation only for the category that included fish, amphibians, and reptiles. Bottom-up regulation may predominate in (primarily terrestrial) systems where resource suitability is more limiting than is resource availability (i.e., resources are defended in some way [especially through incorporation of carbohydrates into indigestible lignin and cellulose]). Top-down regulation may predominate in (primarily aquatic) systems where resources are relatively undefended, or consumers are adapted to defenses, and production can compensate for consumption (D. Strong 1992, see also Chapter 12).

Whereas density dependence acts in a regulatory (stabilizing) manner through negative feedback (i.e., acting to slow or stop continued growth), inverse density dependence has been thought to act in a destabilizing manner. Allee (1931) first proposed that positive feedback creates unstable thresholds (i.e., an extinction threshold below which a population inevitably declines to extinction and the release threshold above which the population grows uncontrollably until resource depletion or epizootics decimate the population) (Begon and Mortimer 1981, Berryman 1996, 1997, Isaev and Khlebopros 1979). Between these thresholds, density-dependent factors should maintain stable populations near K, a property known as the *Allee effect.* However, positive feedback may ensure population persistence at low densities and is counteracted, in most species, by the effects of crowding, resource depletion, and predation at higher densities

Clearly, conditions that bring populations near release or extinction thresholds are of particular interest to ecologists, as well as to resource managers. Bazykin *et al*. (1997), Berryman *et al*. (1987), and Turchin (1990) demonstrated the importance of time lags to the effectiveness of regulatory factors. They demonstrated that time lags weaken negative feedback and reduce the rigidity of population regulation. Hence, populations that are controlled primarily by factors that operate through delayed negative feedback should exhibit greater amplitude of population fluctuation, whereas populations that are controlled by factors with more immediate negative feedback should be more stable. J. Myers (1988) and Mason (1996) concluded that delayed effects of density-dependent factors can generate outbreak cycles with an interval of about 10 years. For irruptive and cyclic populations, decline to near or below local extinction thresholds may affect the time necessary for population recovery between outbreaks.

III. MODELS OF POPULATION CHANGE

Models are representations of complex phenomena and are used to understand and predict changes in those phenomena. Population dynamics of various organisms, especially insects, are of particular concern as population changes affect human health, production of ecosystem commodities, and the quality of terrestrial and aquatic ecosystems. Hence, development of models to improve our ability to understand and predict changes in insect population abundances has a rich history.

Models take many forms. The simplest are conceptual models that clarify relationships between cause and effect. For example, box-and-arrow diagrams can be used to show which system components interact with each other (e.g., Fig. 1.3). More complex statistical models represent those relationships in quantitative terms (e.g., regression models that depict the relationship between population size and environmental factors; e.g., Figs. 5.3–5.4). Advances in computational technology have led to development of biophysical models that can integrate large datasets to predict responses of insect populations to a variety of interacting environmental variables. Computerized decision-support systems integrate a user interface with component submodels that can be linked in various ways, based on user-provided key words, to provide output that addresses specific questions (e.g., C. Shaw and Eav 1993).

A. Exponential and Geometric Models

The simplest model of population growth describes change in numbers as the initial population size times the per capita rate of increase (see Fig. 6.7) (Berryman 1997, Price 1997). This model integrates per capita natality, mortality, immi-

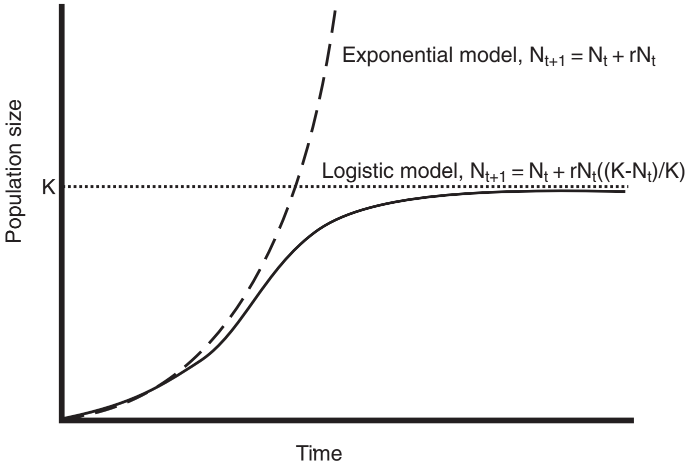


FIG. 6.7 Exponential and logistic models of population growth. The exponential model describes an indefinitely increasing population, whereas the logistic model describes a population reaching an asymptote at the carrying capacity of the environment (K).

gration, and emigration per unit time as the instantaneous or *intrinsic rate of increase*, designated r:

$$r = (N + I) - (M + E) \qquad (6.1)$$

where N = natality, I = immigration, M = mortality, and E = emigration, all instantaneous rates.

Where cohort life table data, rather than time-specific natality, mortality, and dispersal, have been collected, r can be estimated as follows:

$$r = \frac{\log_e R_0}{T} \qquad (6.2)$$

where R_0 is replacement rate, and T is generation time.

The rate of change for populations with overlapping generations is a function of the intrinsic (per capita) rate of increase and the current population size. The resulting model for exponential population growth is as follows:

$$N_{t+1} = N_t + rN_t \qquad (6.3)$$

where N_t is the population size at time t, and N_0 is the initial population size. This equation also can be written as follows:

$$N_t = N_0 e^{rt} \qquad (6.4)$$

For insect species with nonoverlapping cohorts (generations), the replacement rate, R_0, represents the per capita rate of increase from one generation to the next. This parameter can be used in place of r for such insects. The resulting expression for geometric population growth is as follows:

$$N_t = R_0^t N_0 \qquad (6.5)$$

where N_t is the population size after t generations.

Equations 6.3–6.5 describe density-independent population growth (Fig. 6.7). However, as discussed earlier in this chapter, density-dependent competition, predation, and other factors interact to limit population growth.

B. Logistic Model

A mathematic model to account for density-dependent regulation of population growth was developed by Verhulst in 1838 and again, independently, by Pearl and Reed (1920). This logistic model (see Fig. 6.7) often is called the Pearl-Verhulst equation (Berryman 1981, Price 1997). The logistic equation is as follows:

$$N_{t+1} = N_t + rN_t \frac{(K - N_t)}{K} \qquad (6.6)$$

where K is the carrying capacity of the environment. This model describes a sigmoid (S-shaped) curve (see Fig. 6.7) that reaches equilibrium at K. If N < K, then the population will increase up to N = K. If the ecosystem is disturbed in a way that N > K, then the population will decline to N = K.

C. Complex Models

General models such as the Pearl-Verhulst model usually do not predict the dynamics of real systems accurately. For example, the use of the logistic growth model is limited by several assumptions. First, individuals are assumed to be equal in their reproductive potential. Clearly, immature insects and males do not produce offspring, and females vary in their productivity, depending on nutrition, access to oviposition sites, etc. Second, population adjustment to changing density is assumed to be instantaneous, and effects of density-dependent factors are assumed to be a linear function of density. These assumptions ignore time lags, which may control dynamics of some populations and obscure the importance of density dependence (Turchin 1990). Finally, r and K are assumed to be constant. In fact, factors (including K) that affect natality, mortality, and dispersal affect r. Changing environmental conditions, including depletion by dense populations, affect K. Therefore, population size fluctuates with an amplitude that reflects variation in both K and the life history strategy of particular insect species. Species with the r strategy (high reproductive rates and low competitive ability) tend to undergo boom-and-bust cycles because of their tendency to overshoot K, deplete resources, and decline rapidly, often approaching their extinction threshold, whereas species with the K strategy (low reproductive rates and high competitive ability) tend to approach K more slowly and maintain relatively stable population sizes near K (Boyce 1984). Modeling real populations of interest, then, requires development of more complex models with additional parameters that correct these shortcomings, some of which are described as follows.

Nonlinear density-dependent processes and delayed feedback can be addressed by allowing *r* to vary as follows:

$$r = r_{max} - sN_{t-T} \tag{6.7}$$

where r_{max} is the maximum per capita rate of increase, s represents the strength of interaction between individuals in the population, and T is the time delay in the feedback response (Berryman 1981). The sign and magnitude of s also can vary, depending on the relative dominance of competitive and cooperative interactions:

$$s = s_p - s_m N_t \tag{6.8}$$

where s_p is the maximum benefit from cooperative interactions, and s_m is the competitive effect, assuming that s is a linear function of population density at time t (Berryman 1981). The extinction threshold, E, can be incorporated by adding a term forcing population change to be negative below this threshold:

$$N_{t+1} = N_t + rN_t \frac{(K - N_t)}{K} \frac{(N_t - E)}{E} \tag{6.9}$$

Similarly, the effect of factors influencing natality, mortality, and dispersal can be incorporated into the model to improve representation of r.

The effect of other species interacting with a population was addressed first by Lotka (1925) and Volterra (1926). The Lotka-Volterra equation for the effect of a species competing for the same resources includes a term that reflects the degree to which the competing species reduces carrying capacity:

$$N_{1(t+1)} = N_{1t} + r_1 N_{1t} \frac{(K_1 - N_{1t} - \alpha N_{2t})}{K_1} \tag{6.10}$$

where N_1 and N_2 are populations of two competing species, and α is a competition coefficient that measures the per capita inhibitive effect of species 2 on species 1.

Similarly, the effects of a predator on a prey population can be incorporated into the logistic model (Lotka 1925, Volterra 1926) as follows:

$$N_{1(t+1)} = N_{1t} + r_1 N_{1t} - p N_{1t} N_{2t} \tag{6.11}$$

where N_1 is prey population density, N_2 is predator population density, and p is a predation constant. This equation assumes random movement of prey and predator, prey capture and consumption for each encounter with a predator, and no self-limiting density effects for either population (Pianka 1974, Price 1997).

Pianka (1974) suggested that competition among prey could be incorporated by modifying the Lotka-Volterra competition equation as follows:

$$N_{1(t+1)} = N_{1t} + r_1 N_{1t} - \frac{r_1 N_{1t}^2}{K_1} - \frac{r_1 N_{1t} \alpha_{12} N_{2t}}{K_1} \tag{6.12}$$

where α_{12} is the per capita effect of the predator on the prey population. The prey population is density limited as carrying capacity is approached.

May (1981) and Dean (1983) modified the logistic model to include effects of mutualists on population growth. Species-interaction models are discussed more fully in Chapter 8.

Gutierrez (1996) and Royama (1992) discussed additional population-modeling approaches, including incorporation of age and mass structure and population refuges from predation. Clearly, the increasing complexity of these models, as more parameters are included, requires computerization for prediction of population trends.

D. Computerized Models

Computerized simulation models have been developed to project abundances of insect populations affecting crop and forest resources (e.g., Gutierrez 1996, Royama 1992, Rykiel *et al.* 1984). The models developed for several important forest and range insects are arguably the most sophisticated population dynamics models developed to date because they incorporate long time frames, effects of a variety of interacting factors (including climate, soils, host plant variables, competition, and predation) on insect populations, and effects of population change on ecosystem structure and processes. Often, the population dynamics model is integrated with plant growth models; impact models that address effects of population change on ecological, social, and economic variables; and management models that address effects of manipulated resource availability and insect mortality on the insect population (Colbert and Campbell 1978, Leuschner 1980). As more information becomes available on population responses to various factors, or effects on ecosystem processes, the model can be updated, increasing its representation of population dynamics and the accuracy of predictions.

Effects of various factors can be modeled as deterministic (fixed values), stochastic (values based on probability functions), or chaotic (random values) variables (e.g., Croft and Gutierrez 1991, Cushing *et al.* 2003, Hassell *et al.* 1991, Logan and Allen 1992). If natality, mortality, and survival are highly correlated with temperature, these rates would be modeled as a deterministic function of temperature. However, effects of plant condition on these rates might be described best by probability functions and modeled stochastically (Fargo *et al.* 1982, Matis *et al.* 1994).

Advances in chaos theory are contributing to development of population models that more accurately represent the erratic behavior of many insect populations (Cavalieri and Koçak 1994, 1995a, b, Constantino *et al.* 1997, Cushing *et al.* 2003, Hassell *et al.* 1991, Logan and Allen 1992). Chaos theory addresses the unpredictable ways in which initial conditions of a system can affect subsequent system behavior. In other words, population trend at any instant is the result of the unique combination of population and environmental conditions at that instant. For example, changes in gene frequencies and behavior of individuals over time affect the way in which populations respond to environmental conditions. Time lags, nested cycles, and nonlinear interactions with other populations are characteristics of ecological structure that inherently destabilize mathematical models and introduce chaos (Cushing *et al.* 2003, Logan and Allen 1992).

Chaos has been difficult to demonstrate in population models, and its importance to population dynamics is a topic of debate. Dennis *et al.* (2001) demonstrated that a deterministic skeleton model of flour beetle, *Tribolium castaneum*, population dynamics accounted for >92% of the variability in life stage abundances but was strongly influenced by chaotic behavior at certain values for the coefficient of adult cannibalism of pupae (Fig. 6.8).

Several studies suggest that insect population dynamics can undergo recurring transition between stable and chaotic phases when certain variables have values that place the system near a transition point between order and chaos (Cavalieri and Koçak 1995a, b, Constantino *et al.* 1997) or when influenced by a generalist predator and specialist pathogen (Dwyer *et al.* 2004). Cavalieri and Koçak (1994, 1995b) found that small changes in weather-related parameters (increased mortality of pathogen-infected individuals or decreased natality of uninfected individuals) in a European corn borer, *Ostrinia nubilalis*, population dynamics model caused a regular population cycle to become erratic. When this chaotic state was reached, the population reached higher abundances than it did during stable cycles, suggesting that small changes in population parameters resulting from biological control agents could be counterproductive. Although chaotic behavior fundamentally limits long-term prediction of insect population dynamics, improved modeling of transitions between deterministic or stochastic phases and chaotic phases may facilitate prediction of short-term dynamics (Cavalieri and Koçak 1994, Cushing *et al.* 2003, Logan and Allen 1992).

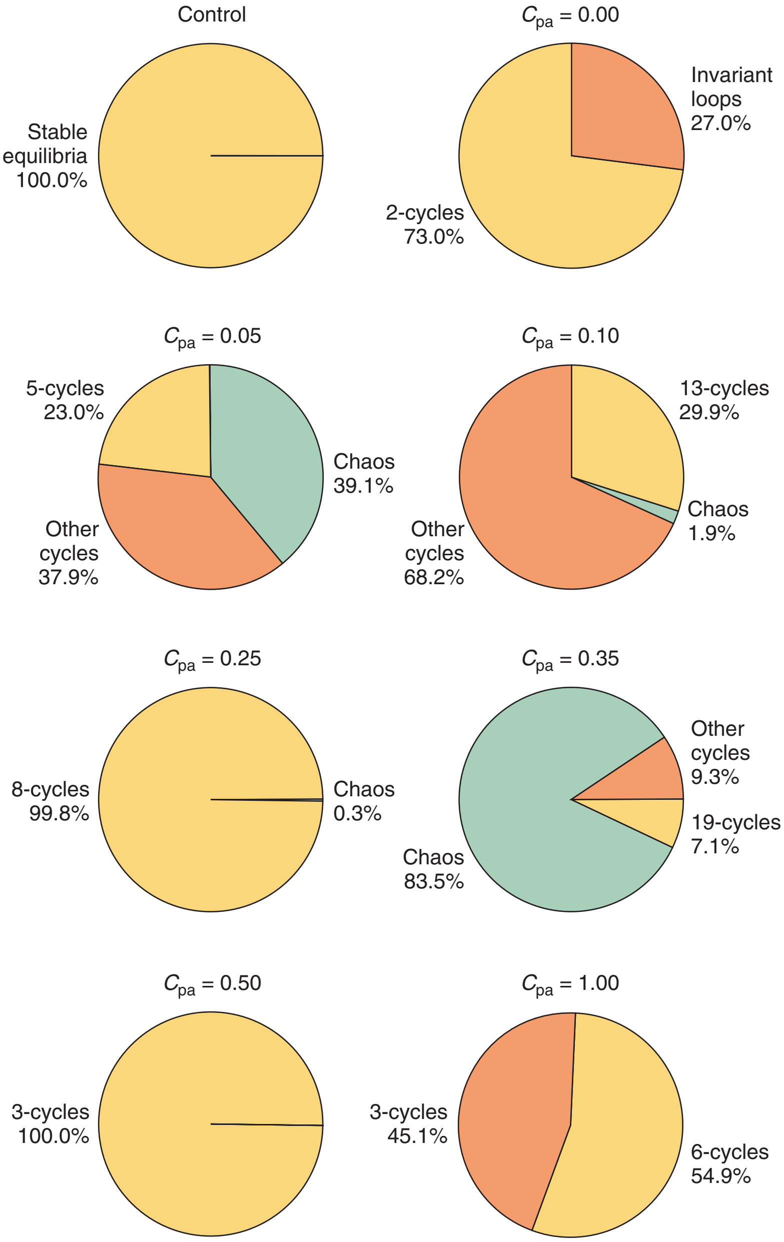


FIG. 6.8 Frequency of predicted deterministic attractors for modeled survival probabilities of pupae in the presence of cannibalistic adults (c_{pa}) of *Tribolium castaneum* for 2000 bootstrap parameter estimates. For example, for $c_{pa} = 0.35$, 83.5% of estimates produced chaotic attractors, 7.1% produced stable 19-cycles, and 9.3% produced stable cycles of higher periods. From Dennis *et al*. (2001) with permission of the Ecological Society of America. Please see extended permission list pg 570.

E. Model Evaluation

The utility of models often is limited by a number of problems. The effects of multiple interacting factors usually must be modeled as the direct effects of individual factors, in the absence of multifactorial experiments to assess interactive effects. Effects of host condition often are particularly difficult to quantify for modeling purposes because factors affecting host biochemistry remain poorly understood for most species. Moreover, models must be initialized with adequate data on current population parameters and environmental conditions. Finally, most models are constructed from data representing relatively short time periods.

Most models accurately represent the observed dynamics of the populations from which the model was developed (e.g., Varley *et al*. 1973), but confidence in their utility for prediction of future population trends under a broad range of environmental conditions depends on proper validation of the model. Validation requires comparison of predicted and observed population dynamics using independent data (i.e., data not used to develop the model). Such comparison using data that represent a range of environmental conditions can indicate the generality of the model and contribute to refinement of parameters subject to environmental influence, until the model predicts changes with a reasonable degree of accuracy (Hain 1980).

Departure of predicted results from observed results can indicate several possible weaknesses in the model. First, important factors may be underrepresented in the model. For example, unmeasured changes in plant biochemistry during drought periods could significantly affect insect population dynamics. Second, model structure may be flawed. Major factors affecting populations may not be appropriately integrated in the model. Finally, the quality of data necessary to initialize the model may be inadequate. Initial values for r, N_0, or other variables must be provided or derived from historic data within the model. Clearly, inadequate data or departure of particular circumstances from tabular data will reduce the utility of model output.

Few studies have examined the consequences of using different types of data for model initialization. The importance of data quality for model initialization can be illustrated by evaluating the effect of several input options on predicted population dynamics of the southern pine beetle. The TAMBEETLE population dynamics model is a mechanistic model that integrates submodels for colonization, oviposition, and larval development with variable stand density and microclimatic functions to predict population growth and tree mortality (Fargo *et al*. 1982, Turnbow *et al*. 1982). Nine variables describing tree (diameter, infested height, and stage of beetle colonization for colonized trees), insect (density of each life stage at multiple heights on colonized trees), and environmental (landform, tree size class distribution and spatial distribution, and daily temperature and precipitation) variables are required for model initialization. Several input options were developed to satisfy these requirements. Options range in complexity from correlative information based on aerial survey or inventory records to detailed information about distribution of beetle life stages and tree characteristics that requires intensive sampling. In the absence of direct data, default values are derived from tabulated data based on intensive population monitoring studies.

Schowalter *et al*. (1982) compared tree mortality predicted by TAMBEETLE using four input options: all data needed for initialization (including life stage and intensity of beetles in trees), environmental data and diameter and height of each colonized tree only, environmental data and infested surface area of each colonized tree only, and environmental data and number of colonized trees only. Predicted tree mortality when all data were provided was twice the predicted mortality when only environmental and tree data were provided and most closely resembled observed beetle population trends and tree mortality.

Insect population dynamics models usually are developed to address "pest" effects on commodity values. Few population dynamics models explicitly incorporate effects of population change on ecosystem processes. In fact, for most insect populations, effects on ecosystem productivity, species composition, hydrology, nutrient cycling, soil structure and fertility, etc., have not been documented. However, a growing number of studies are addressing the effects of insect herbivore or detritivore abundance on primary productivity, hydrology, nutrient cycling, and/or diversity and abundances of other organisms (Klock and Wickman 1978, Leuschner 1980, Schowalter and Sabin 1991, Schowalter *et al*. 1991, Seastedt 1984, 1985, Seastedt and Crossley 1984, Seastedt *et al*. 1988; see also Chapters 12–14). For example, Colbert and Campbell (1978) documented the structure of the integrated Douglas-fir tussock moth, *Orgyia pseudotsugata*, model and the effects of simulated changes in moth density (population dynamics submodel) on density, growth rate, and timber production by tree species (stand prognosis model). Leuschner (1980) described development of equations for evaluating direct effects of southern pine beetle population dynamics on timber, grazing and recreational values, hydrology, understory vegetation, wildlife, and likelihood of fire. Effects of southern pine beetle on these economic values and ecosystem attributes were modeled as functions of the extent of pine tree mortality resulting from changes in beetle abundance. However, for both the Douglas-fir tussock moth and southern pine beetle models, the effects of population dynamics on noneconomic variables are based on limited data.

Modeling of insect population dynamics requires data from continuous monitoring of population size over long time periods, especially for cyclic and irruptive species, to evaluate the effect of changing environmental conditions on population size. However, relatively few insect populations, including pest species, have been monitored for longer than a few decades, and most have been monitored only during outbreaks (e.g., Curry 1994, Turchin 1990). Historic records of outbreak frequency during the past 100–200 years exist for a few species, (e.g., Fitzgerald 1995, Greenbank 1963, Turchin 1990, T. White 1969), and, in some cases, outbreak occurrence over long time periods can be inferred from dendrochronological data in old forests (e.g., Royama 1992, Speer *et al*. 2001, Swetnam and Lynch 1989, Veblen *et al*. 1994). However, such data do not provide sufficient detail on concurrent trends in population size and environmental conditions for most modeling purposes. Data on changes in population densities cover only a few decades for most species (e.g., Berryman 1981, Mason 1996, Price 1997, Rácz and Bernath 1993, Varley *et al*. 1973, Waloff and Thompson 1980). For populations that irrupt infrequently, validation often must be delayed until future outbreaks occur.

Despite limitations, population dynamics models are a valuable tool for synthesizing a vast and complex body of information, for identifying critical gaps in our understanding of factors affecting populations, and for predicting or simulating responses to environmental changes. Therefore, they represent our state-of-the-art understanding of population dynamics, can be used to focus future research on key questions, and can contribute to improved efficiency of management or manipulation of important processes. Population dynamics models are the most rigorous tools available for projecting survival or recovery of endangered species and outbreaks of potential pests and their effects on ecosystem resources.

IV. SUMMARY

Populations of insects can fluctuate dramatically through time, with varying effect on community and ecosystem patterns and processes, as well as on the degree of crowding among members of the population. The amplitude and frequency of fluctuations distinguish irruptive populations, cyclic populations, and stable populations. Cyclic populations have stimulated the greatest interest among ecologists. The various hypotheses to explain cyclic patterns of population fluctuation all include density-dependent regulation with a time lag that generates regular oscillations.

Disturbances are particularly important to population dynamics, triggering outbreaks of some species and locally exterminating others. Disturbances can affect insect populations directly by killing intolerant individuals or indirectly by affecting abundance and suitability of resources or abundance and activity of predators, parasites, and pathogens. The extent to which anthropogenic changes in environmental conditions affect insect populations depends on the degree of similarity between conditions produced by natural versus anthropogenic changes.

Population growth can be regulated (stabilized) to a large extent by density-dependent factors whose probability of effect on individuals increases as density increases and declines as density declines. Primary density-dependent factors are intraspecific competition and predation. Increasing competition for food (and other) resources as density increases leads to reduced natality and increased mortality and dispersal, eventually reducing density. Similarly, predation increases as prey density increases. Although the relative importance of these two factors has been debated extensively, both clearly are critical to population regulation. Regulation by bottom-up factors (resource limitation) may be relatively more important in systems where resources are defended or vary significantly in quality, whereas regulation by top-down factors (predation) may be more important where resources are relatively abundant and show little variation in quality. Inverse density dependence results from cooperation among individuals and represents a potentially destabilizing property of populations. However, this positive feedback may prevent population decline below an extinction threshold. Populations declining below their extinction threshold may be doomed to local extinction, whereas populations increasing above a critical number of individuals (release threshold) continue to increase during an outbreak period. These thresholds represent the minimum and maximum population sizes for species targeted for special management.

Development of population dynamics models has been particularly important for forecasting changes in insect abundance and effects on crop, range, and forest resources. General models include the logistic (Verhulst-Pearl) equation that incorporates initial population size; per capita natality, mortality, and dispersal (instantaneous rate of population change); and environmental carrying capacity. The logistic equation describes a sigmoid curve that reaches an asymptote at carrying capacity. This general model can be modified for particular species by adding parameters to account for nonlinear density-dependent factors, time lags, cooperation, extinction, competition, predation, etc. Models are necessarily simplifications of real systems and may represent effects of multiple interacting factors and chaotic processes poorly. Few models have been adequately validated and fewer have evaluated the effects of input quality on accuracy of predictions. Few population models have been developed to predict effects of insect population dynamics for ecosystem processes other than commodity production. Nevertheless, models represent powerful tools for synthesizing information, identifying priorities for future research, and simulating population responses to future environmental conditions.

7

Biogeography

GEOGRAPHIC RANGES OF SPECIES OCCURRENCE GENERALLY REFLECT THE tolerances of individual organisms to geographic gradients in physical conditions (see Chapter 2). However, most species do not occupy the entire area of potentially suitable environmental conditions. Discontinuity in geographic range reflects a number of factors, particularly geographic barriers and disturbance dynamics. By contrast, suitable habitats can be colonized over large distances from population sources, as a result of dispersal processes, often aided by anthropogenic movement. Factors determining the geographic distribution of organisms have been a particular subject of investigation for the past several centuries (e.g., Andrewartha and Birch 1954, Price 1997), spurred in large part by European and American exploration and floral and faunal collections in continental interiors during the 1800s.

The spatial distribution of populations changes with population size. Growing populations expand over a larger area as individuals in the high-density core disperse to the fringe of the population or colonize new patches. Declining populations shrink into refuges that maintain isolated demes of a metapopulation. Spatial distribution of populations is influenced to a considerable extent by anthropogenic activities that determine landscape structure and introduce (intentionally or unintentionally) commercial and "pest" species to new regions. Changes in insect presence or abundance may be useful biological indicators of ecosystem conditions across landscapes or regions, depending on the degree of habitat specialization of particular species (Rykken *et al*. 1997). Changes in the presence and abundance of particular species affect various ecosystem properties, encouraging efforts to predict changes in distributions of insect populations.

I. GEOGRAPHIC DISTRIBUTION

Geographic distribution of species populations can be described over a range of scales. At the largest scale, some species have population distributions that span large areas of the globe, including multiple continents. At smaller scales, individual species may occur in a suitable portion of a biome or in suitable patches scattered across a biome or landscape. At the same time, species often are absent from apparently suitable habitats. The geographic distribution of individual species can change as a result of changing conditions or dispersal.

A. Global Patterns

Global patterns of distribution reflect latitudinal gradients in temperature and moisture and natural barriers to dispersal. A. Wallace (1876) identified six relatively distinct faunal assemblages that largely coincide with major continental boundaries but also reflect the history of continental movement, as discussed later in this section. Wallace's *biogeographic realms* (Fig. 7.1) remain a useful template for describing species distributions on a global scale. Many taxa occupy large areas within a particular biogeographic realm (e.g., the unique Australian flora and fauna). Others, because of the narrow gap between the Palearctic and Nearctic realms, were able to cross this barrier and exhibit a Holarctic distribution pattern. Of course, many species occupy much smaller geographic ranges, limited by topographic barriers or other factors.

Some distribution patterns, especially of fossil species, are noticeably disjunct. Hooker (1847, 1853, 1860) was among the first to note the similarity of floras found among lands bordering the southern oceans, including Antarctica, Australia, Tasmania, New Zealand, Tierra del Fuego, and the Falklands. Many genera,

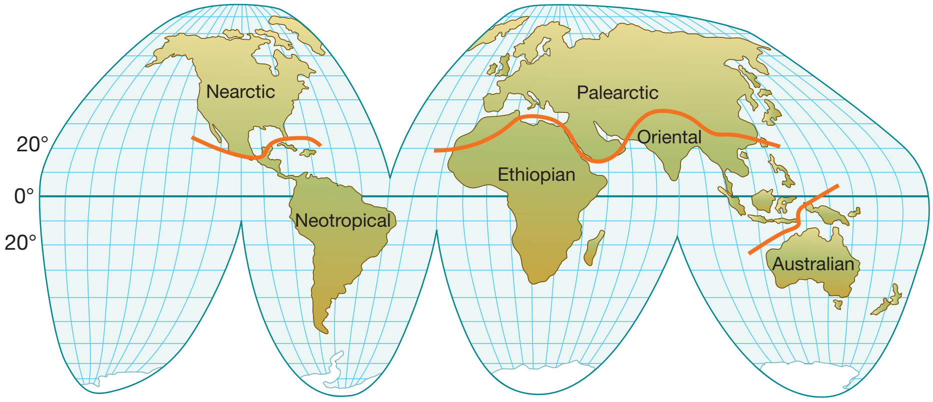


FIG. 7.1 Biogeographic realms identified by A. Wallace (1876).

and even some species, of plants were shared among these widely separated lands, suggesting a common origin.

Later in the 1800s, evidence of stratigraphic congruence of various plant and animal groups among the southern continents supported a hypothetical separation of northern and southern supercontinents. Wegener (1924) was the first to outline a hypothetical geologic history of drift for all the continents, concentrated during Cenozoic time. Wegener's *continental drift hypothesis* was criticized because this history appeared to be incompatible with nonmarine paleontology. However, a growing body of geologic and biological evidence, including stratigraphic congruence, rift valleys, uplift and subsidence zones, and distributions of both extinct and extant flora and fauna, eventually was unified into the *theory of plate tectonics*.

According to this theory, a single landmass (Pangaea) split about 200 million years ago and separated into northern (Laurasia) and southern (Gondwanaland) supercontinents that moved apart as a result of volcanic upwelling in the rift zone. About 135 million years ago India separated from Gondwanaland, moved northward, and eventually collided with Asia to form the Himalaya Mountains. Africa and South America separated about 65 million years ago, prior to the adaptive radiation of angiosperms and mammalian herbivores. South America eventually rejoined North America at the Isthmus of Panama, permitting the placental mammals that evolved in North America to invade and displace the marsupials (other than the generalized opossum) that had continued to dominate South America. Marsupials largely disappeared from the other continents as well, except for Australia, where they survived by virtue of continued isolation. South American flora and fauna moved northward through tropical Central America. This process of continental movement explains the similarity of fossil flora and fauna among the Gondwanaland-derived continents and differences among biogeographic realms (e.g., *Nothofagus* forests in southern continents vs. *Quercus* forests in northern continents).

Continental movements result from the stresses placed on the Earth's crust by planetary motion. Fractures appear along lines of greatest stress and are the basis for volcanic and seismic activity, two powerful forces that lead to displacement of crustal masses. The mid-oceanic ridges and associated volcanism mark the original locations of the continents and preserve evidence of the direction and rate of continental movements. Rift valleys and fault lines usually provide depressions for development of aquatic ecosystems. Mountain ranges develop along lines of collision and subsidence between plates and create elevational gradients and boundaries to dispersal. Volcanic and seismic activity represents a continuing disturbance in many ecosystems.

B. Regional Patterns

Within biogeographic realms, a variety of biomes can be distinguished on the basis of their characteristic vegetation or aquatic characteristics (see Chapter 2). Much of the variation in environmental conditions that produce biomes at the regional scale is the result of global circulation patterns and topography. Mountain ranges and large rivers may be impassible barriers that limit the distribution of many species. Furthermore, mountains show relatively distinct elevational zonation of biomes (life zones). The area available as habitat becomes more limited at higher elevations. Mountaintops resemble oceanic islands in their degree of isolation within a matrix of lower elevation environments and are most vulnerable to climate changes that shift temperature and moisture combinations upward (see Fig. 5.2).

Geographic ranges for many, perhaps most, species are restricted by geographic barriers or by environmental conditions beyond their tolerance limits. Some insect species have broad geographic ranges that span multiple host ranges (e.g., forest tent caterpillar, *Malacosoma disstria;* Parry and Goyer 2004), whereas others have ranges restricted to small areas (e.g., species endemic to cave ecosystems; Boecklen 1991). Species with large geographic ranges often show considerable genetic variation among subpopulations, reflecting adaptations to regional environmental factors. For example, Istock (1981) reported that northern and southern populations of a transcontinental North American pitcher-plant mosquito, *Wyeomyia smithii,* showed distinct genetically based life history patterns. The proportion of third instars entering diapause increased with latitude, reflecting adaptation to seasonal changes in habitat or food availability. Controlled crosses between northern and southern populations yielded high proportions of diapausing progeny from northern × northern crosses, intermediate proportions from northern × southern crosses, and low proportions from southern × southern crosses for larvae subjected to conditions simulating either northern or southern photoperiod and temperature.

C. Island Biogeography

Ecologists have been intrigued at least since the time of Hooker (1847, 1853, 1860) by the presence of related organisms on widely separated oceanic islands. Darwin (1859) and A. Wallace (1911) later interpreted this phenomenon as evidence of natural selection and speciation of isolated populations following separation or colonization from distant population sources. Simberloff (1969), Simberloff and Wilson (1969), and E. Wilson and Simberloff (1969) found that many arthropod species were capable of rapid colonization of experimentally defaunated islands.

Although the *theory of island biogeography* originally was developed to explain patterns of equilibrium species richness among oceanic islands (MacArthur and Wilson 1967), the same factors and processes that govern colonization of oceanic islands explain rates of species colonization and metapopulation dynamics (see the following section) among isolated landscape patches (Cronin 2003, Hanski and Simberloff 1997, Leisnham and Jamieson 2002, Simberloff 1974, Soulé and Simberloff 1986). Critics of this approach have argued that oceanic islands clearly are surrounded by habitat unsuitable for terrestrial species, whereas terrestrial patches may be surrounded by relatively more suitable patches. Some terrestrial habitat patches may be more similar to oceanic islands than others (e.g., alpine tundra on mountaintops may represent substantially isolated habitats) (Leisnham and Jamieson 2002), as are isolated wetlands in a terrestrial matrix (Batzer and Wissinger 1996), whereas disturbed patches in grassland may be less distinct (but see Cronin 2003). A second issue concerns the extent to which the isolated populations constitute distinct species or metapopulations of a single species (Hanski and Simberloff 1997). The resolution of this issue depends on the degree of heterogeneity and isolation among landscape patches and genetic drift among isolated populations over time.

D. Landscape and Stream Continuum Patterns

Within terrestrial biomes, gradients in climate and geographic factors interacting with the patch scale of disturbances across landscapes produce a shifting mosaic of habitat types that affects the distribution of populations. Local extinction of demes must be balanced by colonization of new habitats as they appear for species to survive. However, colonists can arrive in terrestrial patches from various directions and distances. By contrast, distribution of aquatic species is more constrained by the linear (single-dimension) pattern of water flow. Colonists are more likely to come from upstream (if movement is governed by water flow) or downstream (flying adults), with terrestrial patches between stream systems being relatively inhospitable. Population distributions often are relatively distinct among drainage basins (watersheds), depending on the ability of dispersants to colonize new headwaters or tributaries. Hence, terrestrial and aquatic ecologists have developed different approaches to studying spatial dynamics of populations, especially during the 1980s when *landscape ecology* became a paradigm for terrestrial ecologists (M. Turner 1989) and *stream continuum* became a paradigm for stream ecologists (Vannote *et al.* 1980).

Distribution of populations in terrestrial landscapes, stream continua, and oceanic islands is governed to a large extent by probabilities of extinction versus colonization in particular sites (Fig. 7.2; see Chapter 5). The dispersal ability of a species; the suitability of the patch, island, or stream habitat; and its size and distance from the population source determine the probability of colonization by a dispersing individual (see Fig. 5.5). Island or patch size and distance from population sources influence the likelihood that an insect able to travel a given distance in a given direction will contact that island or patch.

Patch suitability reflects the abundance of resources available to colonizing insects. Clearly, suitable resources must be present for colonizing individuals to survive and reproduce. However, preferences by colonizing individuals also may be important. Hanski and Singer (2001) examined the effect of two host plants, *Plantago* spp. and *Veronica* spp., that varied in their relative abundances among patches, on colonization by the Glanville fritillary butterfly, *Melitaea cinxia.* Colonization success was strongly influenced by the correspondence between relative composition of the two host plants and the relative host use by caterpillars in the source patches (i.e., colonizing butterflies strongly preferred to oviposit on the host plant they had used during larval development). The average annual colonization rate was 5% for patches dominated by the host genus less common

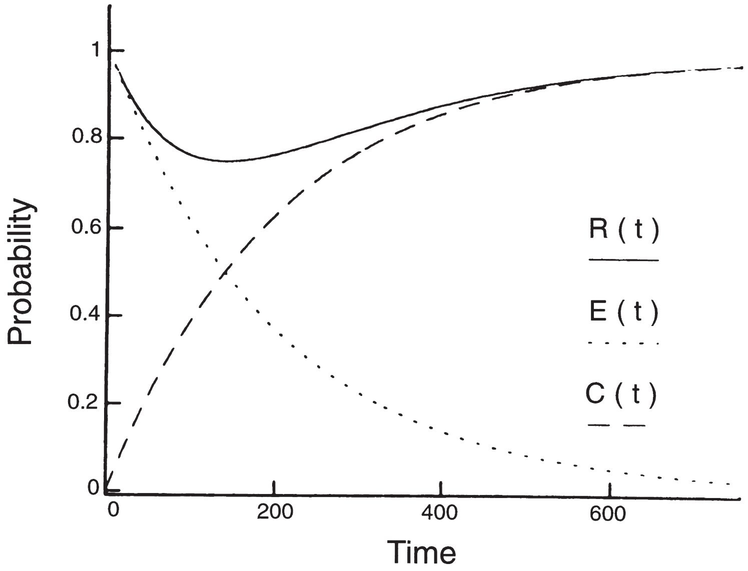


FIG. 7.2 Probability of species presence in an ecosystem (*R*), as a function of probabilities of local extinction (*E*) and colonization (*C*) over time, for specified values of v = probability of colonization over time and λ = probability of extinction over time. From Naeem (1998) with permission from Blackwell Science, Inc. Please see extended permission list pg 570.

across the connecting landscape and 15–20% for patches dominated by the host genus more common across the connecting landscape.

Individual capacity for sustained travel and for detection of cues that facilitate orientation determine colonization ability. Species that fly can travel long distances and traverse obstacles in an aquatic or terrestrial matrix better than can flightless species. Many small insects, including flightless species, catch air currents and are carried long distances at essentially no energetic cost to the insect. J. Edwards and Sugg (1990) reported that a variety of insects could be collected on montane glaciers far from the nearest potential population sources. Torres (1988) reported deposition, by hurricanes, of insect species from as far away as Africa on Caribbean islands.

However, many small, flightless species have limited capacity to disperse. Any factor that increases the time to reach a suitable habitat increases the risk of mortality from predation, extreme temperatures, desiccation, or other factors. Distances of a few meters, especially across exposed soil surfaces, can effectively preclude dispersal by many litter species sensitive to heat and desiccation or vulnerable to predation (Haynes and Cronin 2003). D. Fonseca and Hart (2001) reported that larval black flies, *Simulium vittatum,* were least able to colonize preferred high-velocity habitats in streams because of constraints on their ability to control settlement. Some aquatic species (e.g., Ephemeroptera) have limited life spans as adults to disperse among stream systems. Courtney (1985, 1986) reported that short adult life span was a major factor influencing the common selection of less-suitable larval food plants for oviposition (see Chapter 3). Clearly, the distance between an island or habitat patch and the source population is inversely related to the proportion of dispersing individuals able to reach it (see Fig. 5.5).

Island or patch size and complexity also influence the probability of successful colonization. The larger the patch (or the shorter its distance from the source population), the greater the proportion of the horizon it represents, and the more likely a dispersing insect will be able to contact it. Patch occupancy rate increases with patch size (Cronin 2003). Similarly, the distribution of microsites within landscape or watershed patches affects the ability of dispersing insects to perceive and reach suitable habitats. Basset (1996) reported that the presence of arboreal insects is influenced more strongly by local factors in complex habitats, such as tropical forests, and more strongly by regional factors in less complex habitats, such as temperate forests.

The composition of surrounding patches in a landscape matrix is as important as patch size and isolation in influencing population movement and distribution. Haynes and Cronin (2003) manipulated the composition of the matrix (mudflat, native, nonhost grasses and exotic brome, *Bromus inermis*) surrounding small patches of prairie cordgrass, *Spartina pectinata,* that were identical in size, isolation, and host plant quality. Planthoppers, *Prokelisia crocea,* were marked and released into each host patch. Planthopper emigration rate was 1.3 times higher for patches surrounded by the two nonhost grasses compared to patches surrounded by mudflat (Fig. 7.3). Immigration rate was 5.4 times higher into patches surrounded by brome compared to patches surrounded by mudflat and intermediate in patches surrounded by native nonhost grass. Patch occupancy and density increased with the proportion of the matrix composed of mudflat, probably reflecting the relative inhospitability of the mudflat compared to nonhost grasses.

The increasing rate of dispersal during rapid population growth increases the number of insects moving across the landscape and the probability that some will travel sufficient distance in a given direction to discover suitable patches. Therefore, population contribution to patch colonization and genetic exchange with distant populations is maximized during population growth.

II. SPATIAL DYNAMICS OF POPULATIONS

As populations change in size, they also change in spatial distribution of individuals. Population movement (epidemiology) across landscapes and watersheds (stream continuum) reflects integration of physiological and behavioral attributes with landscape or watershed structure. Growing populations tend to spread across the landscape as dispersal leads to colonization of new habitats, whereas declining populations tend to constrict into more or less isolated refuges. Isolated populations of irruptive or cyclic species can coalesce during outbreaks, facilitating genetic exchange.

Insect populations show considerable spatial variation in densities in response to geographic variation in habitat conditions and resource quality (Fig. 7.4). Variation can occur over relatively small scales because of the small size of insects and their sensitivity to environmental gradients (e.g., Heliövaara and Väisänen 1993, Lincoln *et al*. 1993). The spatial representation of populations can be described across a range of scales from microscopic to global (Chapter 5). The pattern of population distribution can change over time as population size and

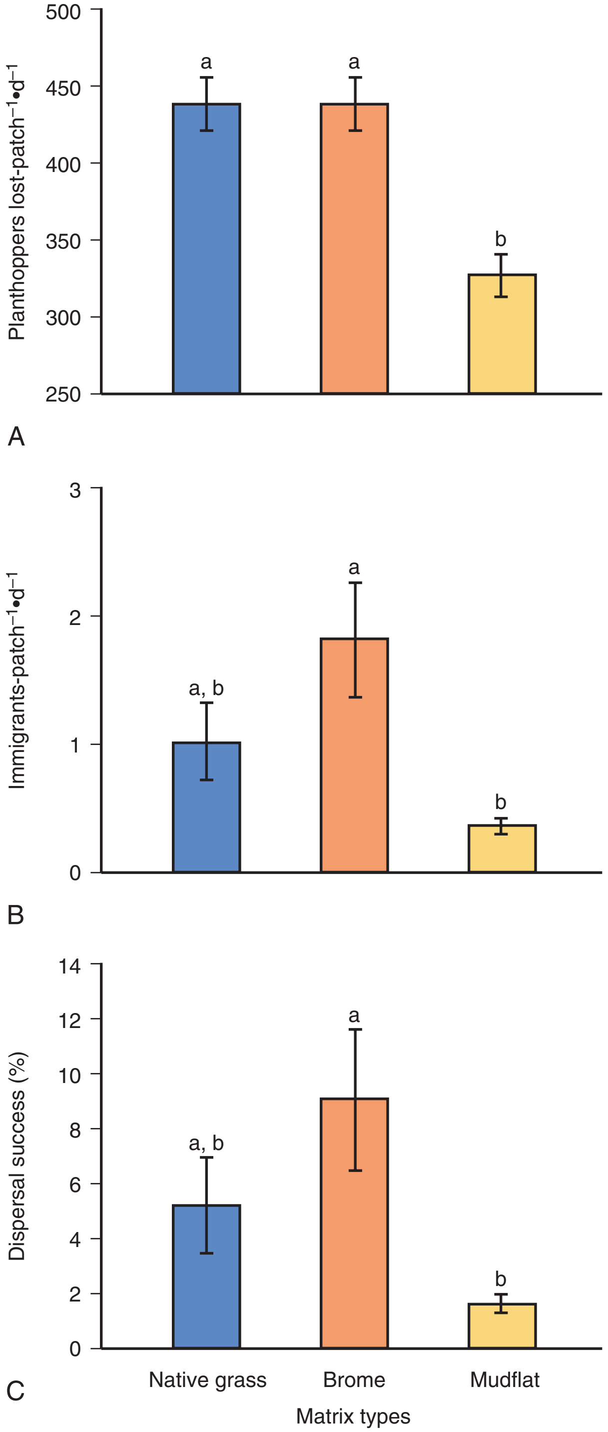


FIG. 7.3 Effect of surrounding matrix on rate of planthopper loss from cordgrass patch in which released (*A*), rate of planthopper immigration into satellite patches (*B*), and percentage of planthoppers lost from the central release patch that successfully immigrated into any of the eight surrounding patches. Vertical lines represent 1 SE. Bars with different letters are significantly different at $P < 0.05$. From Haynes and Cronin (2003) with permission from the Ecological Society of America. Please see extended permission list pg 570.

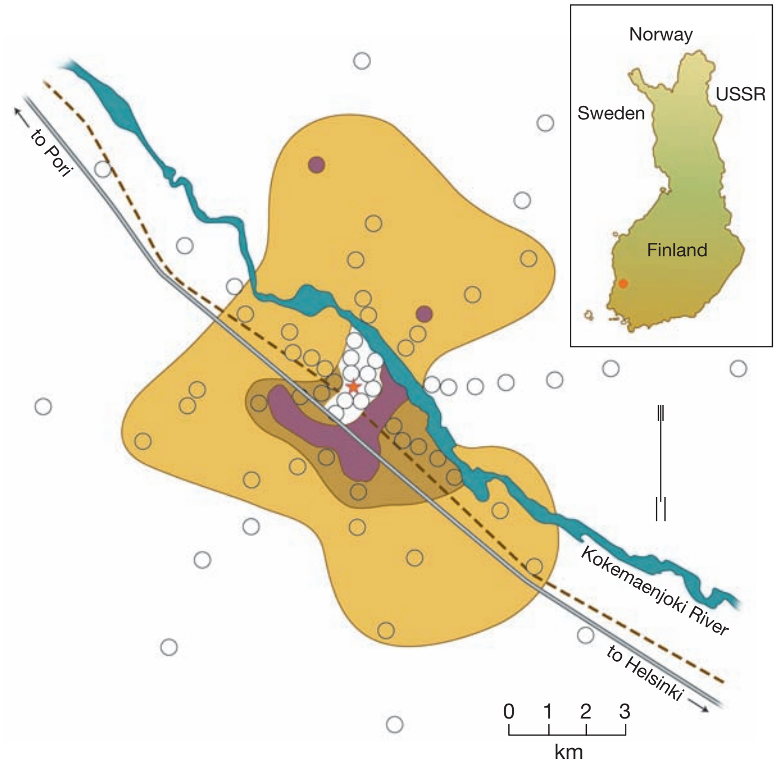


FIG. 7.4 Gradient in pine bark bug, *Aradus cinnamomeus,* densities with distance from the industrial complex (*) at Harjavalta, Finland. White circles = 0–0.50 bugs 100 cm^{-2}, light brown circles = 0.51–1.75 bugs 100 cm^{-2}, brown circles = 1.76–3.50 bugs 100 cm^{-2}, and purple circles = 3.51–12.2 bugs 100 cm^{-2}. From Heliövaara and Väisänen (1986) by permission from Blackwell Wissenschafts-Verlag GmbH.

environmental conditions change. Two general types of spatial variation are represented by the expansion of growing populations and by the discontinuous pattern of fragmented populations, or metapopulations.

A. Expanding Populations

Growing populations tend to spread geographically as density-dependent dispersal leads to colonization of nearby resources. This spread occurs in two ways. First, diffusion from the origin, as density increases, produces a gradient of decreasing density toward the fringe of the expanding population. Grilli and Gorla (1997) reported that leafhopper, *Delphacodes kuscheli,* density was highest within the epidemic area and declined toward the fringes of the population. The difference in density between pairs of sampling points increased as the distance between the sampling points increased. Second, long-distance dispersal leads to colonization of vacant patches and "proliferation" of the population (Hanski and Simberloff 1997). Subsequent growth and expansion of these new demes can lead to population coalescence, with local "hot spots" of superabundance that eventually may disappear as resources in these sites are depleted.

The speed at which a population expands likely affects the efficiency of density-dependent regulatory factors. Populations that expand slowly may experience immediate density-dependent negative feedback in zones of high density, whereas induction of negative feedback may be delayed in rapidly expanding populations because dispersal slows increase in density. Therefore, density-dependent factors should operate with a longer time lag in populations capable of rapid dispersal during irruptive population growth.

The speed, extent, and duration of population spread are limited by the duration of favorable conditions and the homogeneity of the patch or landscape. Populations can spread more rapidly and extensively in homogeneous patches or landscapes such as agricultural and silvicultural systems than in heterogeneous systems in which unsuitable patches limit spread (Schowalter and Turchin 1993). Insect species with annual life cycles often show incremental colonization and population expansion. Disturbances can terminate the spread of sensitive populations. Frequently disturbed systems, such as crop systems or streams subject to annual scouring, limit population spread to the intervals between recolonization and subsequent disturbance. Populations of species with relatively slow dispersal may expand only to the limits of a suitable patch during the favorable period. Spread beyond the patch depends on the suitability of neighboring patches (Liebhold and Elkinton 1989).

The direction of population expansion depends on several factors. The direction of population spread often is constrained by environmental gradients, by wind or water flow, and by unsuitable patches. Gradients in temperature, moisture, or chemical concentrations often restrict the directions in which insect populations can spread, based on tolerance ranges to these factors (Chapter 2). Even relatively homogeneous environments, such as enclosed stored grain, are subject to gradients in internal temperatures that affect spatial change in granivore populations (Flinn *et al.* 1992). Furthermore, direction and flow rate of wind or water have considerable influence on insect movement. Insects with limited capability to move against air or water currents move primarily downwind or downstream, whereas insects capable of movement toward attractive cues move primarily upwind or upstream. Insects that are sensitive to stream temperature, flow rate, or chemistry may be restricted to spread along linear stretches of the stream. Jepson and Thacker (1990) reported that recolonization of agricultural fields by carabid beetles dispersing from population centers was delayed by extensive use of pesticides in neighboring fields.

Schowalter *et al.* (1981b) examined the spread of southern pine beetle, *Dendroctonus frontalis,* populations in east Texas (Fig. 7.5). They described the progressive colonization of individual trees or groups of trees through time by computing centroids of colonization activity on a daily basis (Fig. 7.6). A centroid is the center of beetle mass (numbers) calculated from the weighted abundance of beetles among the x,y coordinates of colonized trees at a given time.

The distances between centroids on successive days was a measure of the rate of population movement (see Fig. 7.6). Populations moved at a rate of 0.9 m/day, primarily in the direction of the nearest group of available trees. However,

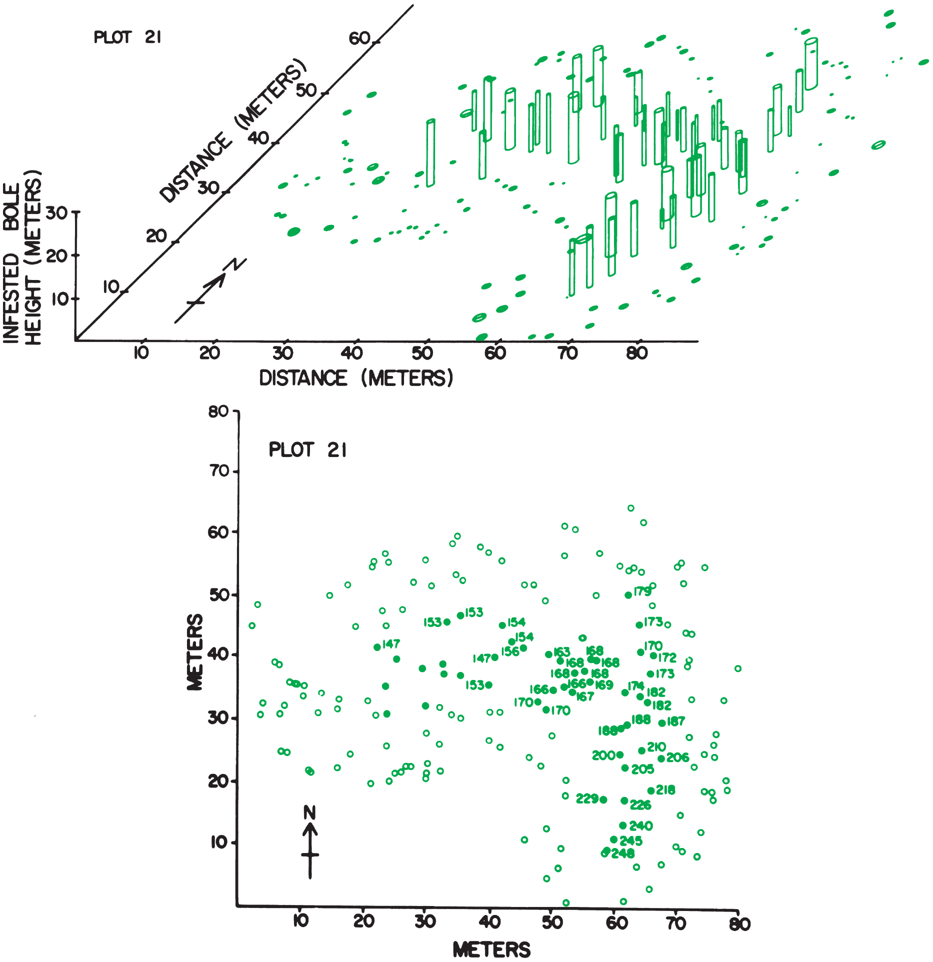


FIG. 7.5 Spatial and temporal pattern of spread of a southern pine beetle population in east Texas during 1977. In the upper figure, cylinders are proportional in size to size of colonized trees; ellipses represent uncolonized trees within 10 m of colonized trees. In the lower figure, Julian dates of initial colonization are given for trees colonized (*solid circles*) after sampling began. Open circles represent uncolonized trees within 10 m of colonized trees. From Schowalter *et al.* (1981b) with permission from the Society of American Foresters.

because southern pine beetle populations generally were sparse during the period of this study, indicating relatively unfavorable conditions, this rate may be near the minimum necessary to sustain population growth.

The probability that a tree would be colonized depended on its distance from currently occupied trees. Trees within 6 m of sources of dispersing beetles had a 14–17% probability of being colonized, compared to a <4% probability for trees further than 6 m from sources of dispersing beetles. Population spread in most cases ended at canopy gaps where no trees were available within 6 m. However,

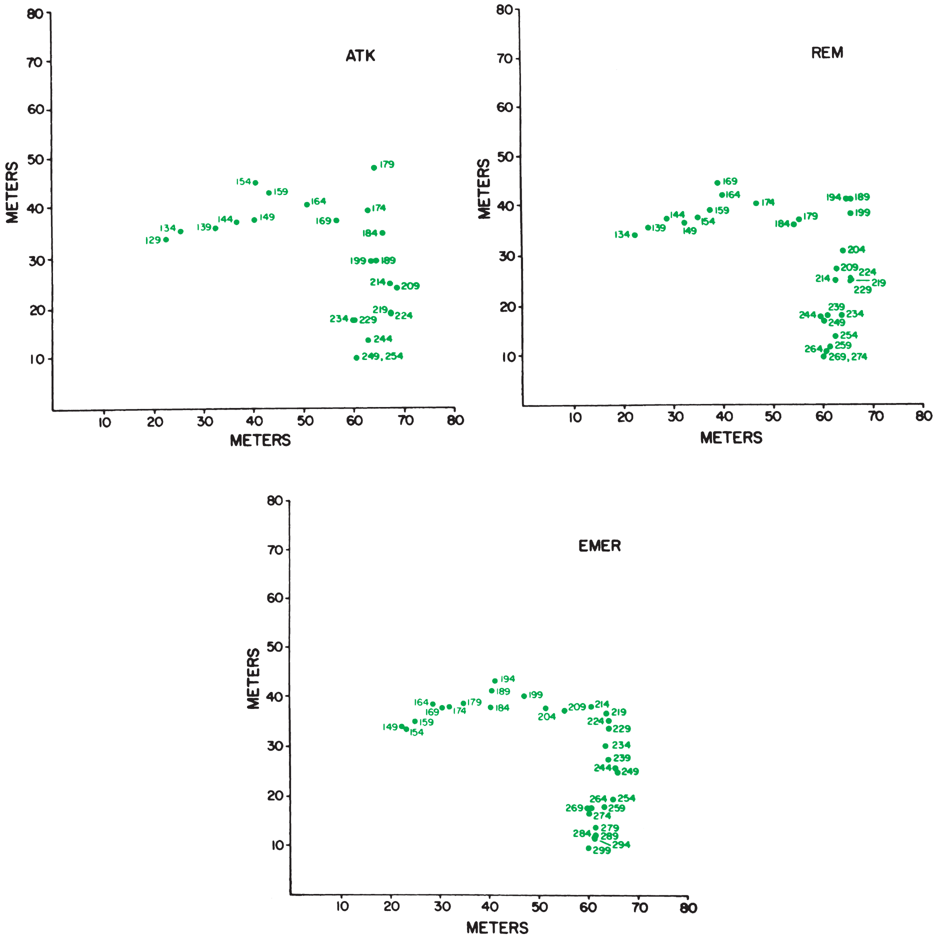


FIG. 7.6 Centroids of colonization (ATK), reemergence (REM), and emergence (EMER), by Julian date, for the southern pine beetle population in Figure 7.4. From Schowalter *et al.* (1981b) with permission from the Society of American Foresters.

one population successfully crossed a larger gap encountered at peak abundance (see Fig. 7.5), indicating that a sufficiently large number of beetles dispersed across the gap to ensure aggregation on suitable trees and sustained population spread.

Population spread in this species may be facilitated by colonization experience and cooperation between cohorts of newly emerging beetles and beetles "reemerging" from densely colonized hosts. Many beetles reemerge after laying some eggs, especially at high colonization densities under outbreak conditions, and seek less densely colonized trees in which to lay remaining eggs. The success of host colonization by southern pine beetles depends on rapid attraction of sufficiently large numbers to overwhelm host defenses (see Chapter 3). For a given day, the centroid of colonization was, on average, twice as far from the centroid of new adults dispersing from brood trees as from the centroid of reemerging beetles (see Fig. 7.6). This pattern suggested that reemerging beetles select the next available trees and provide a focus of attraction for new adults dispersing from farther away.

Related research has reinforced the importance of host tree density for population spread of southern pine beetle and other bark beetles (Amman *et al.* 1988, M. Brown *et al.* 1987, R.G. Mitchell and Preisler 1992, Sartwell and Stevens 1975). Schowalter and Turchin (1993) demonstrated that patches of relatively dense pure pine forest are essential to growth and spread of southern pine beetle populations from experimental refuge trees (see Fig. 6.6). Experimentally established founding populations spread from initially colonized trees surrounded by dense pure pine forest but not from trees surrounded by sparse pines or pine–hardwood mixtures.

A critical aspect of population spread is the degree of continuity of hospitable resources or patches on the landscape. As described in the preceding text for the southern pine beetle, unsuitable patches can interrupt population spread unless population density or growth is sufficient to maintain high dispersal rates across inhospitable patches. Heterogeneous landscapes composed of a variety of patch types force insects to expend their acquired resources detoxifying less acceptable resources or searching for more acceptable resources. Therefore, heterogeneous landscapes should tend to limit population growth and spread, whereas more homogeneous landscapes, such as large areas devoted to plantation forestry, pasture grasses, or major crops, provide conditions more conducive to sustained population growth and spread. However, the particular composition of landscape mosaics may be as important as patch size and isolation in insect movement and population distribution (Haynes and Cronin 2003). Furthermore, herbivores and predators may respond differently to landscape structure. Herbivores were more likely to be absent from small patches than large patches, whereas predators were more likely to be absent from more isolated patches than from less isolated patches in agricultural landscapes in Germany (Zabel and Tscharntke 1998).

Corridors or stepping stones (small intermediate patches) can facilitate population spread among suitable patches across otherwise unsuitable patches. For example, populations of the western harvester ant, *Pogonomyrmex occidentalis,* do not expand across patches subject to frequent anthropogenic disturbance (specifically, soil disruption through agricultural activities) but are able to expand along well-drained, sheltered roadside ditches (DeMers 1993). Roads often provide a disturbed habitat with conditions suitable for dispersal of weedy vegetation and associated insects. Roadside conditions also may increase plant suitability for herbivorous insects and facilitate movement across landscapes fragmented by roads (Spencer and Port 1988, Spencer *et al.* 1988). However, for some insects the effect of corridors and stepping stones may depend on the composition of the surrounding matrix. For example, Baum *et al.* (2004) reported that experimental corridors and stepping stones significantly increased colonization of prairie cordgrass, *S. pectinata,* patches by planthoppers, *P. crocea,* in a low-resistance matrix composed of exotic, nonhost brome, *B. inermis,* that is conducive to planthopper dispersal but not in a high-resistance matrix composed of mudflat that interferes with planthopper dispersal, relative to control matrices without corridors or stepping stones.

Population expansion for many species depends on the extent or duration of suitable climatic conditions. Kozár (1991) reported that several insect species showed sudden range expansion northward in Europe during the 1970s, likely reflecting warming temperatures during this period. Population expansion of spruce budworm (*Choristoneura fumiferana*), western harvester ants, and grasshoppers during outbreaks are associated with warmer, drier periods (Capinera 1987, DeMers 1993, Greenbank 1963).

An important consequence of rapid population growth and dispersal is the colonization of marginally suitable resources or patches where populations could not persist in the absence of continuous influx. Whereas small populations of herbivores, such as locusts or bark beetles, may show considerable selectivity in acceptance of potential hosts, rapidly growing populations often eat all potential hosts in their path. Dense populations of the range caterpillar, *Hemileuca oliviae,* disperse away from population centers as grasses are depleted and form an expanding ring, leaving denuded grassland in their wake. Landscapes that are conducive to population growth and spread, because of widespread homogeneity of resources, facilitate colonization of surrounding patches and more isolated resources because of the large numbers of dispersing insects. Epidemic populations of southern pine beetles, generated in the homogenous pine forests of the southern Coastal Plain during the drought years of the mid-1980s, produced sufficient numbers of dispersing insects to discover and kill most otherwise-resistant pitch pines, *Pinus rigida,* in the southern Appalachian Mountains.

B. Metapopulation Dynamics

A metapopulation is a population composed of relatively isolated demes maintained by some degree of dispersal among suitable patches (Hanski and Simberloff 1997, Harrison and Taylor 1997, Levins 1970). Metapopulation structure can be identified at various scales (Massonnet *et al*. 2002), depending on the scale of distribution and the dispersal ability of the population (Fig. 7.7). For example, metapopulations of some sessile, host-specific insects, such as scale insects (Edmunds and Alstad 1978), can be distinguished among host plants at a local scale, although the insect occurs commonly over a wide geographic range. Local populations of black flies (Simuliidae) can be distinguished at the scale of isolated stream sections characterized by particular substrate, water velocity, temperature, proximity to lake outlets, etc., whereas many species occur over a broad geographic area (e.g., Adler and McCreadie 1997, Hirai *et al*. 1994). Many litter-feeding species occur throughout patches of a particular vegetation type, but that particular vegetation type and associated populations are fragmented at the landscape scale.

Metapopulation structure is most distinct where patches of suitable habitat or food resources are distinct and isolated as a result of natural environmental heterogeneity (e.g., desert or montane landscapes) or anthropogenic fragmentation. The spatial pattern of metapopulations reflects a number of interacting factors, including patch size, isolation, and quality (e.g., resource availability and disturbance frequency) and insect dispersal ability (Fleishman *et al*. 2002), and largely

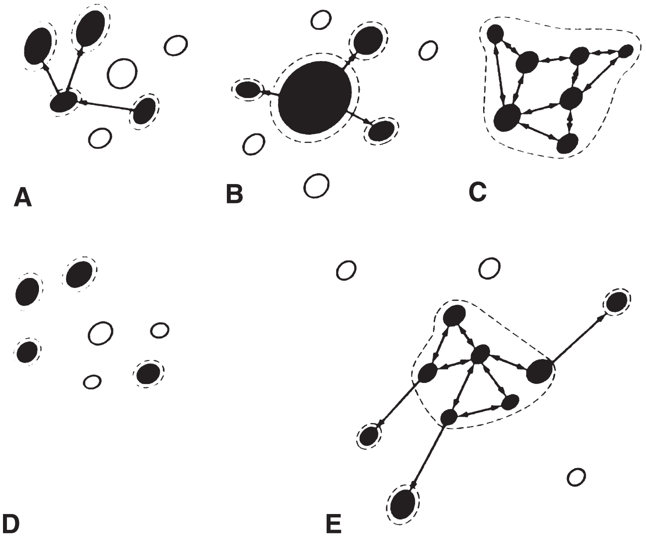


FIG. 7.7 Diagrammatic representation of different metapopulation models. Filled circles are occupied patches; open circles are unoccupied patches; dotted lines are boundaries of local populations; arrows represent dispersal. **A:** Classic (Levins) model of dispersal among demes. **B:** Island biogeography model with the mainland providing a source of colonists. **C:** A network of interacting demes. **D:** A nonequilibrium metapopulation with little capacity for recolonization of vacant patches. **E:** An intermediate case combining features of A–D. From Harrison and Taylor (1997).

determines gene flow; species viability; and, perhaps, evolution of life history strategies (e.g., Colegrave 1997). Hence, attention to spatially structured populations has increased rapidly in recent years.

Metapopulation structure can develop in a number of ways (see Fig. 7.7). One is through the colonization of distant resources and subsequent population development, which occurs during expansion of the source population (see earlier in this chapter). A second is through the isolation of population remnants during population decline. A third represents a stable population structure in a heterogeneous environment, in which vacant patches are colonized as local extinction occurs in other patches.

The colonization of new patches as dispersal increases during population growth is an important mechanism for initiating new demes and facilitating population persistence on the landscape. The large number of dispersants generated during rapid population growth maximizes the probability that suitable resources will be colonized over a considerable area and that more founders will infuse the new demes with greater genetic heterogeneity (Hedrick and Gilpin 1997). Species with ruderal life histories generally exhibit considerable dispersal capacity and often arrive at sites quite remote from their population sources (J. Edwards and Sugg 1990). Such species quickly find and colonize disturbed sites and represent a widely occurring “weedy” fauna. By contrast, species with competitive strategies show much slower rates of dispersal and may travel shorter distances consistent with their more stable population sizes and adaptation to more stable habitats (St. Pierre and Hendrix 2003). Such species can be threatened by rapid changes in environmental conditions that exterminate demes more rapidly than new demes are established (Hanski 1997, Hedrick and Gilpin 1997).

If conditions for population growth continue, the outlying demes may grow and coalesce with the expanding source population. This process contributes to more rapid expansion of growing populations than would occur only as diffusive spread at the fringes of the source population. A well-known example of this is seen in the pattern of gypsy moth, *Lymantria dispar,* population expansion during outbreaks in eastern North America. New demes appear first on ridgetops in the direction of the prevailing wind because of the wind-driven dispersal of ballooning larvae. These demes grow and spread downslope, merging in the valleys. Similarly, swarms of locusts may move great distances to initiate new demes beyond the current range of the population (Lockwood and DeBrey 1990).

As a population retreats during decline, subpopulations often persist in isolated refuges, establishing the postoutbreak metapopulation structure. Refuges are characterized by relatively lower population densities that escape the density-dependent decline of the surrounding population. These surviving demes may remain relatively isolated until the next episode of population growth. The existence and distribution of refuges is extremely important to population persistence. For example, bark beetle populations usually persist as scattered demes in isolated lightning-struck, diseased, or injured trees, which can be colonized by small numbers of beetles (Flamm *et al.* 1993). Such trees appear on the landscape with sufficient frequency and proximity to beetle refuges that endemic populations are maintained (Coulson *et al.* 1983). Croft and Slone (1997) and W. Strong *et al.* (1997) reported that predaceous mites quickly find colonies of spider mites. New leaves on expanding shoots provide important refuges for spider mite colonists by increasing their distance from predators associated with source colonies.

If suitable refuges are unavailable, too isolated, or of limited persistence, a population may decline to extinction. Under these conditions, the numbers and low heterozygosity of dispersants generated by remnant demes are insufficient to ensure viable colonization of available habitats (see Fig. 5.6). For most species, life history strategies represent successful adaptations that balance population processes with natural rates of patch dynamics (i.e., the rates of appearance and disappearance of suitable patches across the landscape). For example, Leisnham and Jamieson (2002) reported that immigration and emigration rates of the mountain stone weta, *Hemideina maori,* were equivalent (0.023 per capita). However, anthropogenic activities have dramatically altered natural rates and landscape pattern of patch turnover and put many species at risk of extinction (Fielding and Brusven 1993, Lockwood and DeBray 1990, Vitousek *et al.* 1997).

Lockwood and DeBray (1990) suggested that loss of critical refuges as a result of anthropogenically altered landscape structure led to the extinction of a previously widespread and periodically irruptive grasshopper species. The Rocky

Mountain grasshopper, *Melanoplus spretus,* occurred primarily in permanent breeding grounds in valleys of the northern Rocky Mountains but was considered to be one of the most serious agricultural pests in western North America prior to 1900. Large swarms periodically migrated throughout the western United States and Canada during the mid-1800s, destroying crops over areas as large as 330,000 km^2 before declining precipitously. The frequency and severity of outbreaks declined during the 1880s, and the last living specimen was collected in 1902. Macroscale changes during this period (e.g., climate changes, reduced activity of Native Americans and bison, and introduction of livestock) do not seem adequate by themselves to explain this extinction. However, the population refuges for this species during the late 1800s were riparian habitats where agricultural activity (e.g., tillage, irrigation, trampling by cattle, introduction of non-native plants and birds) was concentrated. Hence, competition between humans and grasshoppers for refugia with suitable oviposition and nymphal development sites may have been the factor leading to extinction of *M. spretus* (Lockwood and DeBrey 1990).

III. ANTHROPOGENIC EFFECTS ON SPATIAL DYNAMICS

The disappearance of *M. spretus* indicates the vulnerability to extinction of even cyclically abundant species when populations decline to near or below their extinction thresholds (see Chapter 6). Populations always have been vulnerable to local extinctions as a result of disturbances or habitat loss during environmental changes. Species persist to the extent that dispersal capabilities are adapted to the frequency and scale of these changes. Species adapted to relatively unstable habitats usually have higher reproductive rates and greater dispersal capabilities than do species adapted to more stable habitats.

Human activities affect spatial distribution of populations in several ways. Climate changes eventually will force many species to shift their geographic ranges or face extinction as changing temperatures and humidities exceed tolerance ranges or alter energy balance in their current ranges (Franklin *et al.* 1992, Kozár 1991, Rubenstein 1992) (see Fig. 5.2). Changing conditions may favor range expansion for other species. D. Williams and Liebhold (2002) projected that southern pine beetle distribution would shift northward and expand in area with warming climate, whereas mountain pine beetle, *Dendroctonus ponderosae,* distribution would move to higher elevations with shrinking area. D. Williams and Liebhold (1995) found that some climate-change scenarios predicted larger areas of defoliation by gypsy moth, whereas other scenarios predicted smaller areas of defoliation (Fig. 7.8).

Fragmentation of terrestrial ecosystems, alteration and pollution of aquatic ecosystems, and redistribution of species arguably are the most serious and immediate threats to ecosystems worldwide (Samways 1995). Patch scale, distribution, and abruptness of edges have been altered as a result of habitat fragmentation. This has been particularly evident for wetlands and grasslands. Wetlands historically occupied large portions of floodplains but have been virtually eliminated as a result of draining, filling, and stream channelization for

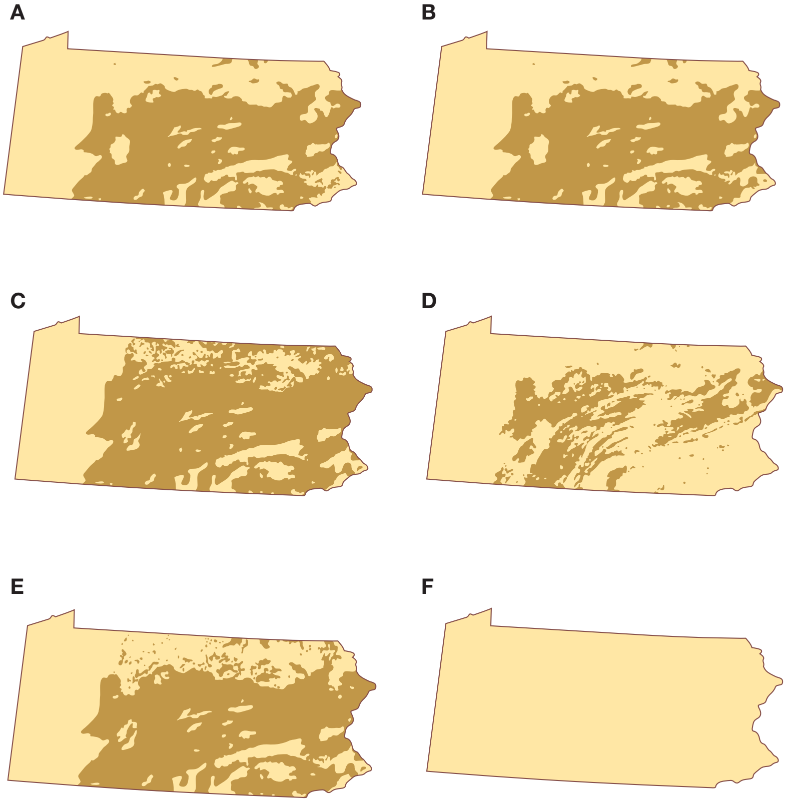


FIG. 7.8 Potential outbreak areas of gypsy moth in Pennsylvania under climate change scenarios. **A:** Current temperature and precipitation; **B:** a 2°C increase; **C:** a 2°C increase and 0.5 mm d^{-1} precipitation increase; **D:** a 2°C increase and 0.5 mm d^{-1} precipitation decrease; **E:** GISS model; and **F:** GFDL model. From D. Williams and Liebhold (1995) with permission from the Entomological Society of America.

urban and agricultural developments. Grasslands have been fragmented severely worldwide because of their suitability for agricultural uses. Reservoirs have altered drainage characteristics and reduced the distances between lake ecosystems. Industrial and agricultural pollution threatens many aquatic species. A large number of vagrant species (including various crops and "weeds," rodents, and livestock, as well as insects and pathogens) have been transported, intentionally and unintentionally, far beyond their natural ranges by human activities. These exotic species have significantly altered the structure and function of their new ecosystems.

A. Fragmentation

Fragmentation is the conversion of contiguous habitat into patches of different habitats or land uses. Habitat fragmentation is especially deleterious to species adapted to relatively stable ecosystems (e.g., Samways 1995) and to rare species (Summerville and Crist 2001). Such species usually are less adapted to rapid or long-distance dispersal and may be less able to recolonize vacant or new habitats (resulting from disturbance or climate change) across inhospitable patches, compared to ruderal species adapted to long-distance colonization of disturbed habitats (St. Pierre and Hendrix 2003, Powell and Powell 1987; see Chapter 5). Furthermore, insects will not be able to colonize new habitat patches successfully until their hosts are established.

Old-growth (500–1000-year-old) conifer forests in Pacific Northwestern North America were substantially fragmented by clearcut harvesting over a 50-year period (1940–1990). The forest landscape changed from about 75% old-growth to about 75% stands <50 years old. A significant proportion of species associated with old-growth forest now exist as relatively small, isolated, and declining populations in a matrix of apparently inhospitable young forest (N. Christensen *et al.* 2000). Schowalter (1995) found that 70% of arboreal arthropod species in old-growth conifer forests in western Oregon were not present in adjacent young (20-year-old) conifer plantations. Predators and detritivores were particularly affected. Similarly, Powell and Powell (1987) found that flower visitation by male euglossine bees declined following forest fragmentation, even in the 100-ha fragment size, and was proportional to fragment size, indicating that very large areas of forest are necessary to maintain viable population sizes for some species.

Whereas fragment size affects persistence of demes, the degree of fragment isolation affects colonization. Steffan-Dewenter and Tscharntke (1999) demonstrated that abundance of pollinating bees and seed production declined with increasing isolation (distance) of experimental mustard, *Sinapis arvensis,* and radish, *Raphanus sativus,* plants from intact grassland in Germany.

Krawchuk and Taylor (2003) studied patterns of abundance of three dipterans, *Wyeomyia smithii* (Culicidae), *Metriocnemus knabi* (Chironimidae), and *Fletcherimyia fletcheri* (Sarcophagidae) inhabiting pitcher plants, *Sarracenia purpurea,* in western Newfoundland, Canada. For all three insect species, habitat configuration (patch size and isolation) was more important than the total area of habitat, but the relative importances of patch size versus isolation changed with spatial scale. Patch size was more important at the scale of movement and survival of individuals, whereas patch isolation was more important at the scale of matrix configuration and metapopulation dynamics.

Edges between patches are particularly pronounced in anthropogenic landscapes and affect dispersal of many species. Natural gradients of climate and geology interacting with disturbances produce relatively large patches, with broad transition zones (ecotones) between patches that dampen interference by one patch on environmental conditions of another. By contrast, human land use practices tend to produce smaller patches with abrupt edges (e.g., distinct agricultural monocultures within fenced boundaries, plowed edges against grasslands, harvested and regenerating plantations against mature forests, and greater edge density measured as edge perimeter (m) per ha) (e.g., Radeloff *et al.* 2000). These distinct edges substantially influence environmental conditions of the adjacent patches. For example, an edge of tall trees along an abrupt boundary with an adjacent plantation of short trees is exposed to much greater insolation and airflow, depending on edge orientation, leading to higher temperatures, lower humidities, and greater vulnerability to windthrow than prevailed when the edge was buffered by forest. J. Chen *et al*. (1995) discovered that microclimatic gradients extended 180–480 m into old-growth Douglas fir, *Pseudotsuga menziesii,* forests from clearcut edges, affecting habitat conditions for associated organisms. They concluded that forest patches <64 ha would be completely compromised by external environmental conditions (i.e., would be characterized entirely as edge habitat rather than as interior forest habitat). Similarly, grasslands overgrazed by livestock within fenced boundaries expose soil to desiccation, leading to death of surrounding vegetation and an increasing area of desertification (e.g., Schlesinger *et al*. 1990, see Fig. 2.8f).

Insects are sensitive to these edge effects. Roland and Kaupp (1995) found that transmission of nuclear polyhedrosis virus was reduced along forest edges, prolonging outbreaks of the forest tent caterpillar, *Malacosoma disstria.* Ozanne *et al*. (1997) documented lower abundances of Psocoptera, Lepidoptera, Coleoptera, Hymenoptera, Collembola, and Araneae and higher abundances of Homoptera and Thysanoptera at forest edges compared to interior forest habitats. Schowalter (1994, 1995) reported that these two groups of taxa generally characterized undisturbed and disturbed forests, respectively. Haynes and Cronin (2003) found that planthoppers, *P. crocea,* accumulated along edges, compared to the interior, of prairie cordgrass patches adjacent to mudflat but not patches adjacent to nonhost grasses, reflecting lower rates of dispersal across inhospitable mudflats (see Fig. 7.3). Similar results were found for understory insectivorous birds in tropical forest, suggesting that outbreaks of some insects could be more likely in fragments from which predators have disappeared (Ṣekereioğlu *et al*. 2002). Remnant patches of natural habitat also are highly vulnerable to influx of nonindigenous species, from neighboring patches, that may compete with, or prey upon, indigenous species (Punttila *et al*. 1994).

Effects of edge density on the landscape can change during the course of population growth and decline. Radeloff *et al*. (2000) found that correlations between landscape patterns and jack pine budworm, *Choristoneura pinus,* population size varied over time, with proportion of jack pine, *Pinus banksiana,* and edge density (sum of perimeter length for land use classes per ha) positively correlated up to the peak of the outbreak, but edge density negatively correlated during population decline. These results probably reflect the more suitable resources represented by pollen cones that are more abundant on edge trees and the greater abundance of avian predators and the primary wasp parasitoid, *Itoplectis conquisitor,* along edges.

Fragmentation does not affect all species equally or all negatively. Tscharntke (1992) reviewed studies that examined responses of several insect species to differences in reed, *Phragmites australis,* quality in fragmented (agricultural) and unfragmented (nature reserve) wetlands. Reeds in small patches had thinner shoots but more leaves than did reeds in large patches. Two chloropid flies, *Lipara* spp., that depend on thin shoots survived only in small patches or in the unmown edges of large patches. However, the stem-boring noctuid moth, *Archanara germinipuncta,* that depends on thick shoots persisted only in large patches. Shoot damage caused by this moth created necessary habitat for >20 other herbivores, saprovores, and parasitoids. For example, the gall midge, *Lasioptera arundinis,* survived only in the side shoots induced by *A. germinipucta* damage, making this midge equally dependent on large patches. Tscharntke (1992) calculated that survival of local populations of *A. germinipuncta* requires at least 180,000 individuals or at least a 2-ha area.

Fragmentation of natural ecosystems usually is associated with homogenization of vegetation patterns. Widespread planting of commercial crops and suppression of natural disturbances have eliminated much of the diversity of vegetation patches characterizing natural landscapes. In a diverse landscape, outbreaks of particular demes most often would be confined to patches of susceptible vegetation. Agricultural and forested landscapes have become more conducive to expansion and regionwide outbreaks of adapted species (Schowalter and Turchin 1993).

B. Disturbances to Aquatic Ecosystems

Stream channelization and impoundment have reduced heterogeneity in channel morphology and flow characteristics. Channelization constrains channel morphology, removes obstacles to flow, and shortens stream length. These modifications eliminate habitats in overflow areas (such as wetlands and side channels) and in logs and other impediments and accelerate drainage in the channeled sections. Impoundments replace a sequence of turbulent sections and pools behind logs and other obstacles (characterized by rocky substrates and high oxygen contents) with deep reservoirs (characterized by silty substrates and stratification of oxygen content and temperature). These changes in stream conditions eliminate habitat for some species (such as species associated with high flow rate and oxygen concentrations) and increase habitat availability for others (such as species associated with lotic condition and low oxygen concentrations).

The linear configuration of stream systems (i.e., the stream continuum concept; Vannote *et al.* 1980) makes them particularly vulnerable to disturbances that occur upstream. For example, heavy precipitation in the watershed is concentrated in the stream channel, scouring the channel and redistributing materials and organisms downstream. Fire or harvest of riparian vegetation exposes streams or wetlands to increased sunlight, raising temperatures and increasing primary production, altering habitat and resource conditions downstream, often for long time periods (Batzer *et al.* 2000a, Haggerty *et al.* 2004). Industrial effluents, runoff of agricultural materials (e.g., fertilizers), or accidental inputs of toxic materials (e.g., pesticides) affect habitat suitability downstream until sufficient dilution has occurred (S. Smith *et al.* 1983, Southwick *et al.* 1995). Eutrophication, resulting from addition of limiting nutrients, substantially alters the biological and chemical conditions of aquatic systems.

Lake Balaton (Europe's largest lake) in Hungary has experienced incremental eutrophication since the early 1960s, when lake chemistry was relatively uniform (Somlyódy and van Straten 1986). Since that time, phosphorus inputs from agricultural runoff and urban development have increased, starting at the west end where the Zala River enters the lake. The division of Lake Balaton into four relatively distinct basins draining distinct subwatersheds facilitated documentation of the progression of eutrophication from west to east (Somlyódy and van Straten 1986). Dévai and Moldován (1983) and Ponyi *et al*. (1983) found that the abundance and species composition of chironomid larvae were correlated with this longitudinal gradient in water quality. The original species characterizing oligomesotrophic conditions have been replaced by species characterizing eutrophic conditions in a west-to-east direction. Similarly, sedimentation resulting from erosion of croplands or clearcut forests or from trampling of streambanks by livestock alters substrate conditions and habitat suitability for organisms downstream.

Pringle (1997) reported that disturbances and anthropogenic modification of downstream areas (e.g., urbanization, channelization, impoundment, etc.) also affect conditions for organisms upstream. Degraded downstream areas may be more vulnerable to establishment of exotic species that are tolerant of stream degradation. These species subsequently invade upstream habitats. Degradation of downstream areas may restrict movement of upstream species within the watershed, thereby isolating headwater populations and limiting gene flow between watersheds. Finally, degradation of downstream zones may prevent movement of anadromous or catadromous species.

Disturbances to adjacent terrestrial ecosystems affect aquatic species. Davies and Nelson (1994) compared aquatic invertebrate responses to forest harvest within 10 m of streams, 10–30 m of streams, 30–50 m of streams, or unharvested in Tasmania. Densities of aquatic invertebrates were measured at a site upstream of the treatment and at a second site immediately downstream from the treatment. Differences in mayfly (Ephemeroptera) and stonefly (Plecoptera) densities between the two sites were significantly, negatively correlated with width of the riparian forest buffer. Overall, mayfly density declined 62% and stonefly density declined 34% at sites with <30 m of buffer, demonstrating the importance of riparian forest buffers to aquatic species.

C. Species Introductions

Human transportation of exotic species across natural barriers to their dispersal has altered dramatically the structure and function of natural ecosystems across the globe (Samways 1995, A. Suarez *et al*. 1998, Wallner 1996). Examples include the devastation of island vegetation by pigs and goats introduced intentionally by explorers; destruction of grasslands globally by domesticated, often introduced, livestock; disruption of aquatic communities by introduced amphibians, fish, and mollusks (e.g., African clawed frog and zebra mussel in North America); and disruption of grassland and forest communities by introduced plants (e.g., spotted knapweed in North America), mammals (e.g., rabbits in Australia), reptiles (brown tree snake in Oceania), insects (e.g., gypsy moth in North America, the European wood wasp, *Sirex noctulio,* in Australia), and pathogens (e.g., chestnut blight and white pine blister rust in North America, Dutch elm disease in North America and Europe, pinewood nematode in Japan). Exotic species, especially of insects, can be found in virtually all "natural" ecosystems on all continents. Many herbivorous insects and mites have arrived on agricultural or forestry products and become plant pests in agroecosystems or forests. Some herbivorous and predaceous arthropods have been introduced intentionally for biological control of exotic weeds or plant pests (e.g., Croft 1990, Kogan 1998, McEvoy *et al*. 1991). Despite evaluation efforts, these biological control agents, especially arthropod predators, compete with native species and have the potential to colonize native hosts related to the exotic host and develop new biotypes. Indigenous herbivore species also can colonize exotic hosts and develop new biotypes (D. Strong *et al*. 1984), with unknown consequences for long-term population dynamics and community structure. Samways *et al*. (1996) found that different invertebrate assemblages were found on exotic vegetation, compared to indigenous vegetation, in South Africa.

Urban areas represent increasingly large and interconnected patches on regional landscapes and are particularly important ports for the spread of exotic species into surrounding ecosystems. Urban centers are the origin or destination for commercial transport of a wide variety of materials, including forest and agricultural products. Urban areas are characterized by a wide variety of exotic species, especially ornamental plants and their associated exotic insects and pathogens. Exotic or native ornamental species usually are stressed by soil compaction, air and water pollutants, elevated urban temperatures, etc. Arriving exotics often have little difficulty finding suitable hosts and becoming established in urban centers and subsequently spreading into surrounding ecosystems.

Road systems connecting urban centers and penetrating natural ecosystems represent major corridors that facilitate spread of exotic species. Roadsides usually are highly disturbed by road maintenance, other human activities, and air pollution from vehicles and provide suitable habitat for a variety of invasive species. Gypsy moth is particularly capable of spreading via human transportation (of pupae or egg masses attached to vehicles, outdoor equipment, or commercial products) between urban centers. Stiles and Jones (1998) demonstrated that population distribution of the red imported fire ant, *Solenopsis invicta,* was significantly affected by width and disturbance frequency of road and powerline corridors through forests in the southeastern United States (Fig. 7.9). Mound densities were significantly highest along dirt roads not covered by forest canopy and lowest along roads covered by forest canopy. Powerline and graveled or paved roads not covered by forest canopy supported intermediate densities of mounds. These trends suggest that canopy openings of intermediate width and high disturbance frequency are most conducive to fire ant colonization.

IV. CONSERVATION BIOLOGY

A growing number of species are becoming vulnerable to extinction as populations shrink and become more isolated in disappearing habitats (Boecklen 1991, M. Wilson *et al*. 1997) or are displaced by exotic competitors. Examples include a number of butterfly species, the American burying beetle, *Necrophorus americanus,* and a number of aquatic and cave-dwelling species (e.g., Boecklen 1991,

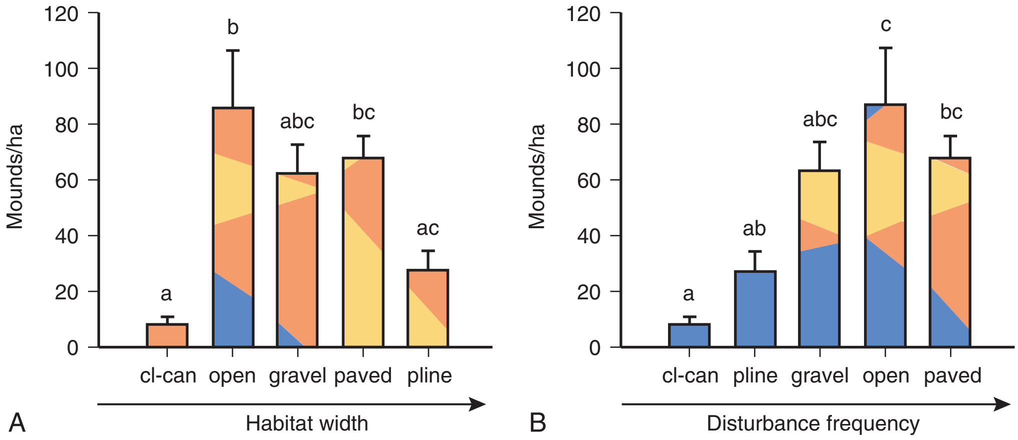


FIG. 7.9 Mean (+ standard error) density of fire ant, *Solenopsis invicta,* mounds along roads under various canopy and substrate conditions in order of increasing corridor width (*a*) and disturbance frequency (*b*) at the Savanna River Site in South Carolina. cl-can = closed canopy, pline = powerline cut, and open, gravel, and paved = open canopy roads with dirt, gravel, or paved surfaces, respectively. N = 10 for each treatment. Bars with different letters are significantly different at $p < 0.05$. From Stiles and Jones (1998) with permission from Kluwer Academic Publishers.

Hanski and Simberloff 1997, C. Thomas and Hanski 1997, M. Wilson *et al.* 1997). All of these species are vulnerable to extinction because of their rarity and the increasing fragmentation and isolation of their habitats. Maintenance or recovery of endangered species requires attention to the size and distribution of nature reserves for remnant populations.

The theory of island biogeography was a dominating paradigm in conservation biology during the 1970s and 1980s and continues to shape perspectives of nature reserves as habitat islands (e.g., Diamond and May 1981, Harris 1984). One of the important early applications of this theory was to the development of rules for refuge design. The most widely debated of these rules was the SLOSS (single large or several small) rule, based on the likelihood of colonization and persistence of large versus small islands or patches. Diamond and May (1981) noted that the value of various options for species viability depended on the habitat area required by a species and its dispersal capability. Small organisms such as insects could persist in smaller reserves than could larger organisms such as vertebrates. In fact, insects often can persist undetected on rare hosts in relatively small, isolated patches, as was the case for Fender's blue butterfly, *Icaricia icarioides fenderi.* This species was last seen in 1936 before being rediscovered in 1989 in small remnant patches of its host lupine, *Lupinus sulphureus kincaidii,* in western Oregon (M. Wilson *et al.* 1997). Nevertheless, species in disappearing habitats remain vulnerable to extinction, as in the case of the Rocky Mountain grasshopper (Lockwood and DeBrey 1990).

Island biogeography theory has largely been supplanted by models of metapopulation dynamics. Metapopulation models are based on the landscape pattern of demes and gene flow among demes in a nonequilibrium landscape (Hanski and Simberloff 1997, Harrison and Taylor 1997). Small demes are most vulnerable to local extinction as a result of disturbances, but their presence may be critical to recolonization of vacant patches or gene exchange with nearby demes. Dispersal among patches is critical to maintaining declining populations and preventing or delaying local extinction. Clearly, population recovery for such species depends on restoration or replacement of habitats.

Principles of metapopulation dynamics may be particularly important for conservation and restoration of populations of entomophagous predators and parasites in landscapes managed for ecosystem commodities (e.g., forestry and agricultural products). Predators and parasitoids are recognized as important natural agents of crop pest regulation but as a group appear to be particularly vulnerable to habitat fragmentation (Kruess and Tscharntke 1994, Schowalter 1995) and pesticide application (Sherratt and Jepson 1993). Hassell *et al*. (1991) and Sherratt and Jepson (1993) suggested that predator and parasite persistence in agroecosystems depends on the metapopulation dynamics of their prey, as well as on the frequency and distribution of pesticide use, and that connectivity between patches characterized by locally unstable predator–prey interactions could allow their mutual persistence. M. Thomas *et al*. (1992) found that creation of islands of grassland habitats in agricultural landscapes increased the abundances of several groups of entomophagous arthropods.

Corridors connecting otherwise-isolated habitat patches have been identified as critical needs for conservation biology. Just as roads and other disturbed corridors facilitate movement of invasive species among disturbed habitats (DeMers 1993, Spencer and Port 1988, Spencer *et al*. 1988), corridors of undisturbed habitat connecting undisturbed patches can facilitate movement of species characterizing these habitats.

Várkonyi *et al*. (2003) used mark–recapture techniques to track movement of two species of noctuid moths, *Xestia speciosa,* a habitat generalist that can be found in natural and managed spruce forests and also in pine-dominated forest throughout Finland, and *X. fennica,* a species more restricted to natural spruce forests in northern Finland. They found that both species preferred to move along spruce forest corridors and avoid entering the matrix of clearcuts and regenerating forest. Movement of *X. speciosa* generally covered longer distances, whereas movement of *X. fennica* was characterized by shorter distances confined within corridors. However, *X. fennica* was capable of longer-distance dispersal across the matrix.

Haddad (1999, 2000) demonstrated that corridors between patches of open-habitat, embedded in pine, *Pinus* spp., forest significantly increased interpatch dispersal of buckeye, *Junonia coenia,* and variegated fritillary, *Euptoieta claudia,* butterflies (Fig. 7.10). Haddad and Baum (1999) found that three butterfly species (*J. coenia, E. claudia,* and cloudless sulphur, *Phoebis sennae*) characterizing open habitat reached higher population densities in patches connected by corridors than in isolated patches; a fourth species, the spicebush swallowtail, *Papilio troilus,* did not show any preference for open versus pine habitat and did not differ in density between connected or isolated patches. Collinge (2000) also reported variable effects of corridors on grassland insect movement. Corridors slightly increased the probability of colonization by less vagile species but did not affect recolonization by rare species. One of three focus species significantly

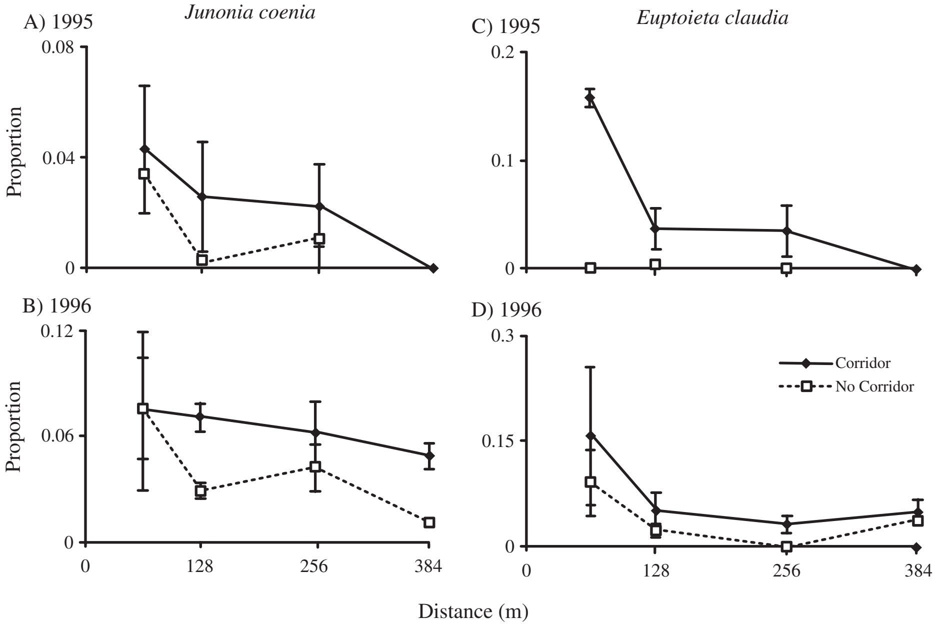


FIG. 7.10 Proportion of marked butterflies, *Junonia coenia* and *Euptoieta claudia,* that moved increasing distances to adjacent patches connected by a corridor or unconnected. From Haddad (1999) with permission from the Ecological Society of America. Please see extended permission list pg 570.

preferred corridors, whereas the other two moved independently of corridors. These studies indicated that corridors may facilitate movement of organisms among patches, but their effect depends on species characteristics, landscape context, patch size, corridor length, and environmental variation.

Riparian corridors have been a focus of many conservation efforts for some vertebrates, but few studies have addressed arthropod responses to riparian corridors. Riparian vegetation has been shown to protect stream or wetland conditions and maintain aquatic species (Batzer *et al.* 2000a, Davies and Nelson 1994, Haggerty *et al.* 2004, M. Stone and Wallace 1998). Davies and Nelson (1994) reported 34–62% declines in mayfly and stonefly densities in streams with riparian buffers <30-m wide, compared to streams with buffers >50-m wide (see earlier in this chapter). Cartron *et al.* (2003) found that carabid beetle abundance and species richness were significantly higher in riparian forests subject to periodic flooding, compared to nonflooded sites, indicating the importance of flooding for some riparian taxa. The distinct habitat characterizing riparian corridors may not be suitable for conserving upland species in areas with steep elevational gradients.

V. MODELS OF SPATIAL DYNAMICS

The most significant advance in population dynamics research in recent years has been the development of spatially explicit models of population dynamics.

A number of approaches have been used to model spatial dynamics. As with temporal dynamics, spatial dynamics can be modeled using deterministic, stochastic, or chaotic functions (Hassell *et al*. 1991, Matis *et al*. 1994, Sherratt and Jepson 1993). Different spatial dynamics result from using these different types of functions.

The earliest attempts to model spatial dynamics either applied diffusion models to describe insect dispersal and population spread from population centers (Rudd and Gandour 1985, Skellam 1951, Turchin 1998) or modeled population dynamics independently among individual landscape patches, based on local conditions within each patch, and linked patches by dispersal processes (e.g., W. Clark 1979). Diffusion models assume that the environment is homogeneous and that individuals disperse independently and with equal probability in any direction. The diffusion approach is useful for modeling spatial dynamics of insects in stored grain or relatively homogenous crop systems but less useful in most natural landscapes where patchiness interrupts diffusion.

Advances in spatial modeling have been facilitated by development of powerful computers that can store and manipulate large datasets. Concurrent development of geographic positioning systems (GPS) and geographic information systems (GIS) and geostatistical software has been a key to describing insect movement (Turchin 1998) and population epidemiology (Liebhold *et al*. 1993) across landscapes.

A GIS is an integrated set of programs that facilitate collection, storage, manipulation, and analysis of geographically referenced data, such as topography, vegetation type and density, and insect population densities. Data for a particular set of coordinates can be represented as a value for a cell, and each cell in the matrix is given a value (Fig. 7.11). This method is called the *Raster method.* A second method, which requires less storage space, is the *vector method* in which only data representing the vertices of polygons containing data must be stored (see Fig. 7.11). Various matrices representing different map layers can be superimposed to analyze interactions. For example, a map layer representing insect population distribution can be superimposed on map layers representing the distribution of host plants, predator abundances, climatic conditions, disturbances, or topography to evaluate the effects of patchiness or gradients in these factors on the spatial dynamics of the insect population.

Geostatistics are a means of interpolating the most probable population densities between sample points to improve representation of spatial distribution over landscapes. Early attempts to characterize spatial patterns were based on modifications of s^2/x, Taylor's Power Law, Lloyd's Patchiness Index, and Iwao's patchiness regression coefficients (Liebhold *et al*. 1993). These indices focus on frequency distributions of samples and are useful for identifying dispersion patterns (see Chapter 5), but they ignore the spatial locations of samples. Modeling spatial dynamics across landscapes requires information on the location of sampling points, as well as population-density data. The locations of population aggregations affect densities in adjacent cells (Coulson *et al*. 1996, Liebhold and Elkinton 1989). Development of GPS has facilitated incorporation of precise sample locations in GIS databases.

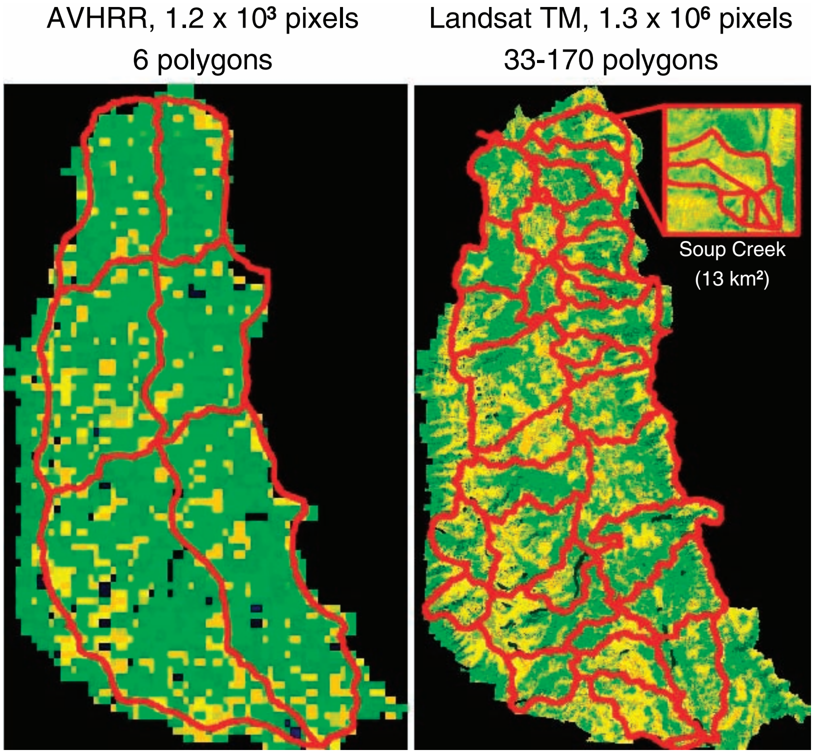


FIG. 7.11 Examples of geostatistical representation. The Seeley-Swan watershed in Montana, United States, is depicted with 1-km^2 raster cells on the left, by 30 × 30 m raster cells on the right, and with vector polygons defined from topographic analysis in the inset. The more heterogeneneous the landscape, the greater the number of cells required to provide an accurate assessment of spatial variation. From R. Waring and Running (1998). Please see extended permission list pg 570.

An underlying assumption of geostatistics is that the degree of similarity between sample points is correlated with their proximity (Fig. 7.12) (Coulson *et al.* 1996, Gilbert and Grégoire 2003, Grilli and Gorla 1997, Liebhold *et al.* 1993, M. Smith *et al.* 2004). Population structure in a given cell is influenced by the population structures in neighboring cells more than by distant cells. An autocorrelation matrix can be developed from data for different distance classes (i.e., x and y coordinates differing by a given distance; Liebhold and Elkinton 1989). This spatial autocorrelation can be used to interpolate values for unsampled locations by taking a weighted linear average of available samples, a technique known as kriging (Gilbert and Grégoire 2003, Gribko *et al.* 1995, Grilli and Gorla 1997, Hohn *et al.* 1993, Liebhold *et al.* 1993). Kriging represents an advance over traditional methods of interpolation in several ways, but its most important provision is incorporation of several forms of information simultaneously. The joint spatial dependence of population density and factors such as climate, soil conditions, vegetation, etc. can be integrated to provide more accurate estimates than would be possible with any single variable.

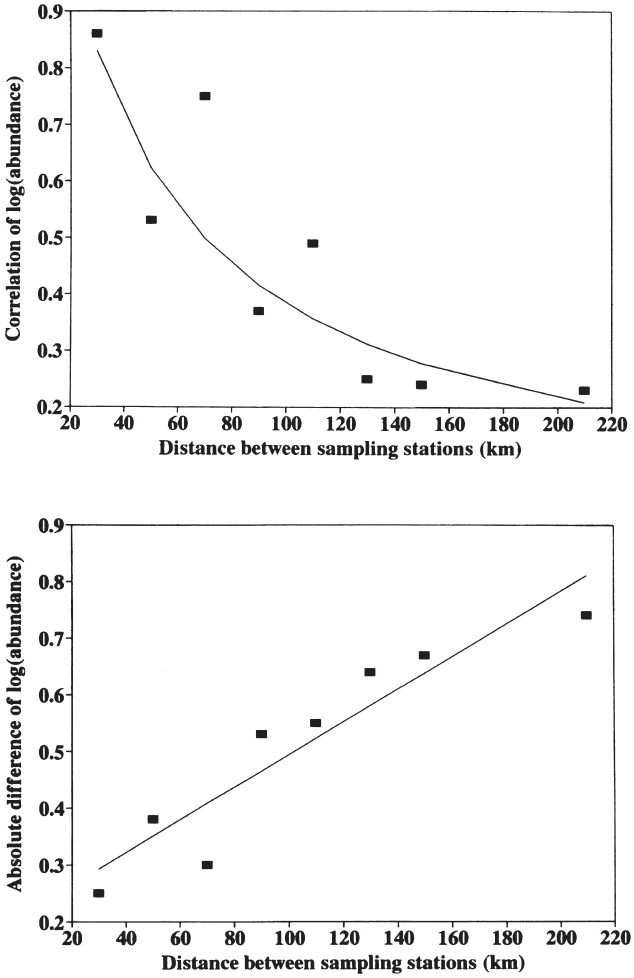


FIG. 7.12 Relationships for the temporal correlation of *Delphacodes kuscheli* density and the distance between sampling stations (*top*) and for the mean absolute difference in densities for pairs of sampling stations and the distance between sampling stations (*bottom*) in Argentina. From Grilli and Gorla (1997) with permission from CAB International.

Gilbert and Grégoire (2003) used these methods to evaluate factors affecting the spatial structure of the European bark beetle, *Dendroctonus micans,* in a French spruce forest (Fig. 7.13). They demonstrated that the *D. micans* population had a strong spatial structure, significantly related to tree density; average slope within a 250-m radius; and the number of the specialist predator, *Rhizophagus grandis,* released within a 300-m radius >6 years previously. D. Williams and Liebhold (1995) used these techniques to predict the spatial distribution of insect population densities under potential future climates (see Fig. 7.8).

Modeling of spatial dynamics in stream networks or montane topography with branched topology presents special challenges. In such networks, the distance between two points may not be represented adequately by Euclidean distance

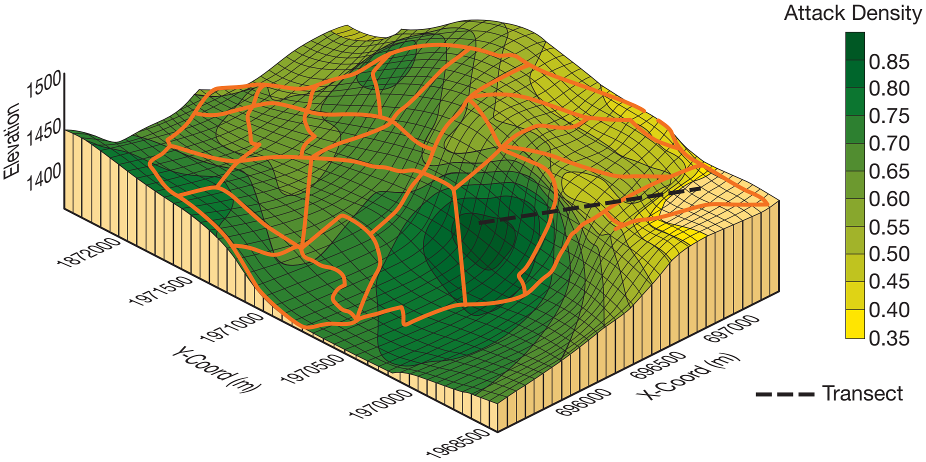


FIG. 7.13 Spatial structure of proportion of trees attacked by *Dendroctonus micans,* based on two-dimensional omni-directional kriging, in a 600-ha spruce stand in France. From Gilbert and Grégoire (2003) with permission from the Royal Entomological Society. Please see extended permission list pg 570.

because of limitations to movement of aquatic organisms across land. Rather, the shortest distance from the perspective of aquatic organisms is along the stream channel (Fig. 7.14a). Ganio *et al.* (2005) described use of an empirical variogram, based on shortest distances along the network pathway between sample points, to evaluate spatial patterns and differences in spatial structure along stream networks in western Oregon, United States (Fig. 7.14b). Such new tools will contribute to modeling of spatial structure in aquatic populations.

VI. SUMMARY

Factors affecting the geographic distributions of populations have intrigued ecologists for at least the past two centuries. Distributions can be described at different geographic scales. Six distinctive floral and faunal associations (biogeographic realms) can be identified, conforming roughly to continental boundaries but also reflecting the history of continental movement (plate tectonics). Topography also creates gradients in environmental conditions on mountains and temperature stratification with depth in aquatic ecosystems.

The distribution of species among islands intrigued early ecologists. The ability of populations to colonize oceanic islands was found to reflect the dispersal capacity of the species, the size of the island, and its distance from the population source. Although controversial, principles of island biogeography have been applied to colonization of terrestrial habitat islands (e.g., mountaintops and patches of unique habitat in otherwise inhospitable landscapes).

At more local scales, the spatial distribution of populations changes with population size. Growing populations expand over a larger area as individuals move from high-density patches to the fringe of the population. Rapidly expanding populations generate large numbers of dispersing individuals that maximize the

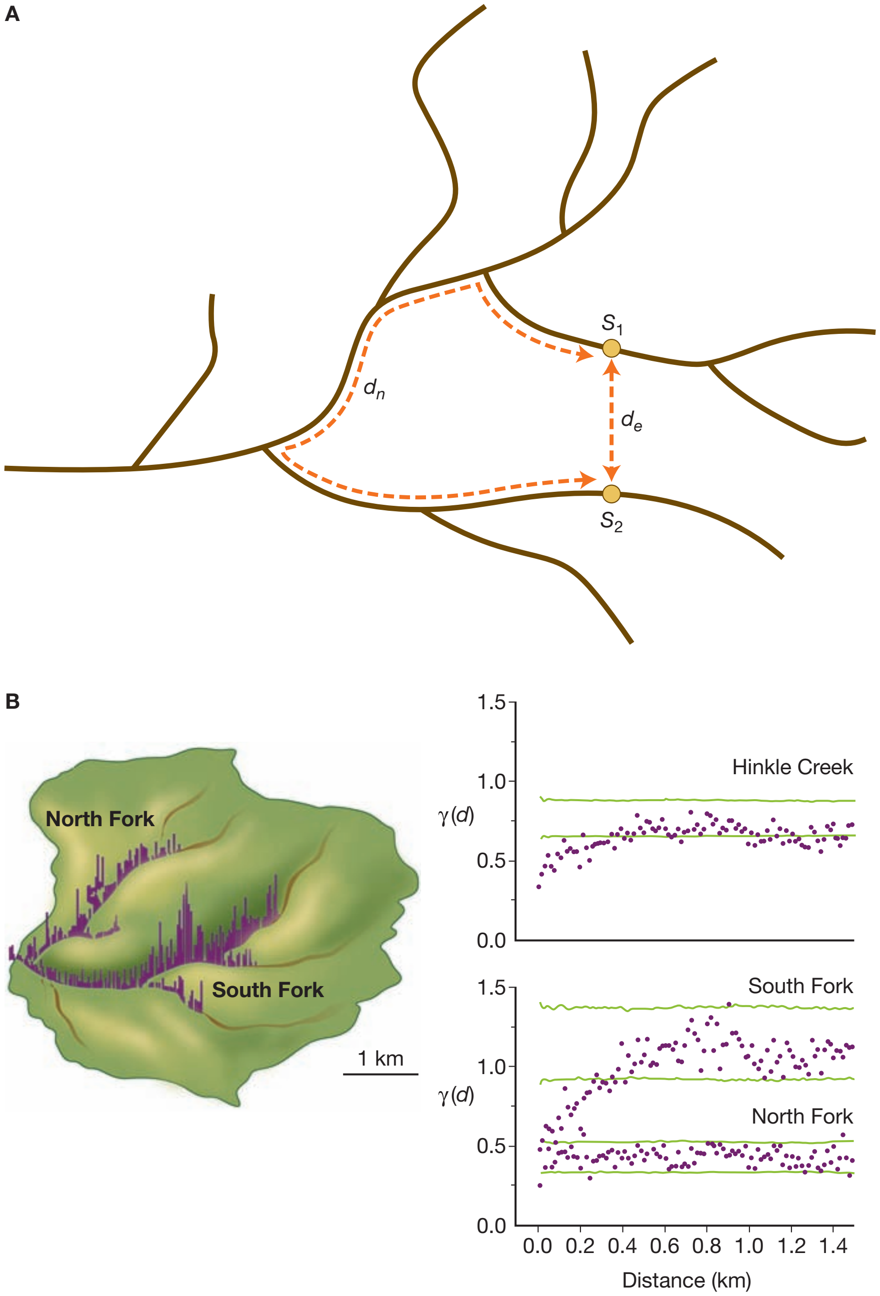


FIG. 7.14 **A:** Distance between points s_1 and s_2 in a network can be measured either as Euclidean distance (d_e) or as distance along the network pathway (d_n); **B:** Spatial distribution and empiric variograms of coastal cutthroat trout counts in Hinkle Creek in western Oregon. Variograms show semivariance as a function of network distance (d_n) with 2.5th and 97.5th percentiles from 5000 permutations (*green lines*) for the entire watershed and for the North and South forks separately. From Ganio *et al*. (2005) with permission from the Ecological Society of America. Please see extended permission list pg 570.

colonization of new patches. Under favorable conditions, these satellite demes expand and coalesce with the main population, affecting ecosystem processes over large areas. Declining populations shrink into isolated refuges that maintain distinct demes of a metapopulation. The extent of movement of individuals among these demes determines genetic heterogeneity and ability to recolonize patches following local extinctions.

All populations are vulnerable to local extinctions as a result of changing environmental conditions and disturbances. Populations survive to the extent that their dispersal strategies facilitate recolonization and population movement over landscapes. Anthropogenic activities alter spatial distribution in several ways. Climate changes affect the geographic distribution of suitable habitats. However, the most serious anthropogenic effects on spatial patterns are habitat fragmentation, alteration and pollution of aquatic ecosystems, and redistribution (intentionally or unintentionally) of various species. Fragmentation increases isolation of demes and places many species at risk of extinction. At the same time, predators and parasites appear to be most vulnerable to fragmentation and habitat disturbances, often increasing opportunities for population growth by prey species. Humans also are responsible for the introduction of a large and growing number of plant and animal species to new regions as a result of transportation of commercial species and forest and agricultural products. Urban areas represent centers of commercial introductions and provide opportunities for exotic ornamental and associated species to become established and move into surrounding ecosystems. These species affect various ecosystem properties, often dramatically altering vegetation structure and competing with, or preying on, native species.

Modeling of spatial distribution patterns has been facilitated by development of GIS and geostatistical techniques. Early models represented population expansion as a simple diffusion process. Application of GIS techniques to the patch dynamics of metapopulations permits integration of data on population dynamics with data on other spatially varying factors across landscapes. Geostatistical techniques, such as kriging, permit interpolation of density data between sampling stations to improve mapping and projecting of population distributions. These techniques are improving our ability to evaluate population contributions to ecosystem properties across landscapes.

SECTION III

COMMUNITY ECOLOGY

SPECIES CO-OCCURRING AT A SITE INTERACT TO VARIOUS degrees, both directly and indirectly, in ways that have intrigued ecologists since earliest times. These interactions represent mechanisms that control population dynamics, hence community structure, and also control rates of energy and matter fluxes, hence ecosystem function. Some organisms engage in close, direct interactions, as consumers and their hosts, whereas others interact more loosely and indirectly. For example, predation on mimics depends on the presence of their models, and herbivores are affected by their host's chemical or other responses to other herbivores. Direct interactions (i.e., competition, predation, and symbioses) have been the focus of research on factors controlling community structure and dynamics, but indirect interactions also control community organization. Species interactions are the focus of Chapter 8.

A community is composed of the plant, animal, and microbial species occupying a site. Some of these organisms are integral and characteristic components of the community and help define the community type, whereas others occur by chance as a result of movement across a landscape or through a watershed. For example, certain combinations of species (e.g., ruderal, competitive, or stress-tolerant) distinguish desert, grassland, or forest communities. Different species assemblages are found in turbulent water (stream) versus standing water (lake) or eutrophic versus oligotrophic systems. The number of species and their relative abundances define species diversity, a community attribute that is the focus of a number of ecological issues. Chapter 9 addresses the various approaches to describing community structure and factors determining geographic patterns of community structure.

Communities change through time as populations respond differently to changing environmental conditions, especially to disturbances. Just as population dynamics reflect the net effects of individual natality, mortality, and dispersal interacting with the environment, community dynamics reflect the net effects of species population dynamics interacting with the environment. Severe disturbance or environmental changes can lead to drastic changes in community structure. Changes in community structure through time are the subject of a vast literature summarized in Chapter 10.

Community structure largely determines the biotic environment affecting individuals (Section I) and populations (Section II). The community modifies the environmental conditions of a site. Vegetation cover reduces albedo (reflectance of solar energy), reduces soil erosion, modifies temperature and humidity within the boundary layer, and alters energy and biogeochemical fluxes, compared to nonvegetated sites. Species interactions, including those involving insects, modify vegetation cover and affect these processes, as discussed in Section IV. Different community structures affect these processes in different ways.

8

Species Interactions

JUST AS INDIVIDUALS INTERACT IN WAYS THAT AFFECT POPULATION structure and dynamics, species populations in a community interact in ways that affect community structure and dynamics. Species interactions vary considerably in their form, strength, and effect and often are quite complex. One species can influence the behavior or abundance of another species directly (e.g., a predator feeding on its prey) or indirectly through effects on other associated species (e.g., an herbivore inducing production of plant chemicals that attract predators or deter feeding by herbivores arriving later). The web of interactions, direct and indirect and with positive or negative feedbacks, determines the structure and dynamics of the community (see Chapters 9 and 10) and controls rates of energy and matter fluxes through ecosystems (see Chapter 11).

Insects have provided rich fodder for studies of species interactions. Insects are involved in all types of interactions, as competitors, prey, predators, parasites, commensals, mutualists, and hosts. The complex and elaborate interactions between insect herbivores and host plants and between pollinators and their hosts have been among the most widely studied. Our understanding of plant–herbivore, predator–prey, animal–fungus, and various symbiotic interactions is derived largely from models involving insects. This chapter describes the major classes of interactions, factors that affect these interactions, and consequences of interactions for community organization.

I. CLASSES OF INTERACTIONS

Species can interact in various ways and with varying degrees of intimacy. For example, individuals compete with, prey on, or are prey for various associated species and may be involved in more specific interactions with particular species (i.e., symbiosis). Categories of interactions generally have been distinguished on the basis of the sign of their direct effects (i.e., positive, neutral, or negative effects) on growth or mortality of each species. However, the complexity of indirect effects on interacting pairs of species by other associated species has become widely recognized. Furthermore, interactions often have multiple effects on the species involved, depending on abundance and condition of the partners, requiring consideration of the net effects of the interaction to understand its origin and consequences.

A. Competition

Competition is the struggle for use of shared, limiting resources. Resources can be limiting at various amounts and for various reasons. For example, water or nutrient resources may be largely unavailable and support only small populations or a few species in certain habitats (e.g., desert and oligotrophic lakes) but be abundant and support larger populations or more species in other habitats (e.g., rainforest and eutrophic lakes). Newly available resources may be relatively unlimited until sufficient colonization has occurred to reduce per capita availability. Any resource can be an object of interspecific competition (e.g., basking or oviposition sites, food resources, etc.).

Although competition for limited resources has been a major foundation for evolutionary theory (Malthus 1789, Darwin 1859), its role in natural communities has been controversial (e.g., Connell 1983, Lawton 1982, Lawton and Strong 1981, Schoener 1982, D. Strong *et al.* 1984). Denno *et al.* (1995) and Price (1997) attributed the controversy over the importance of interspecific competition to three major criticisms that arose during the 1980s. First, early studies were primarily laboratory experiments or field observations. Few experimental field studies were conducted prior to the late 1970s. Second, Hairston *et al.* (1960) argued that food must rarely be limiting to herbivores because so little plant material is consumed under normal circumstances (see also Chapter 3). As a result, most field experiments during the late 1970s and early 1980s focused on effects of predators, parasites, and pathogens on herbivore populations. Third, many species assumed to compete for the same resource(s) co-occur and appear not to be resource limited. In addition, many communities apparently were unsaturated (i.e., many niches were vacant; e.g., Kozár 1992b, D. Strong *et al.* 1984). The controversy during this period led to more experimental approaches to studying competition. Some (but not all) experiments in which one competitor was removed have demonstrated increased abundance or resource use by the remaining competitor(s) indicative of competition (Denno *et al.* 1995, Istock 1973, 1977, Pianka 1981). However, many factors affect interspecific competition (Colegrave 1997), and Denno *et al.* (1995) and Pianka (1981) suggested that competition may operate over a gradient of intensities, depending on the degree of niche partitioning (see later in this section).

Denno *et al.* (1995) reviewed studies involving 193 pairs of phytophagous insect species. They found that 76% of these interactions demonstrated competition, whereas only 18% indicated no competition, although they acknowledged that published studies might be biased in favor of species expected to compete. The strength and frequency of competitive interactions varied considerably. Generally, interspecific competition was more prevalent, frequent, and symmetrical among haustellate (sap-sucking) species than among mandibulate (chewing) species or between sap-sucking and chewing species. Competition was more prevalent among species feeding internally (e.g., miners and seed-, stem-, and wood-borers; Fig. 8.1) than among species feeding externally. Competition was observed least often among free-living, chewing species (i.e., those generally emphasized in earlier studies that challenged the importance of competition).

FIG. 8.1 Competition: evidence of interference between southern pine beetle, *Dendroctonus frontalis,* larvae (small mines) and co-occurring cerambycid, *Monochamus titillator,* larvae (larger mines) preserved in bark from a dead pine tree. The larger cerambycid larvae often remove phloem resources in advance of bark beetle larvae, consume bark beetle larvae in their path, or both.

Most competitive interactions (84%) were asymmetrical (i.e., one species was a superior competitor and suppressed the other) (Denno *et al.* 1995). Root feeders were consistently out-competed by folivores, although this, and other, competitive interactions may be mediated by host plant factors (see later in this chapter). Istock (1973) demonstrated experimentally that competition between two waterboatmen species was asymmetrical (Fig. 8.2). Population size of *Hesperocorixa lobata* was significantly reduced when *Sigara macropala* was present, but population size of *S. macropala* was not significantly affected by the presence of *H. lobata.*

Competition generally is assumed to have only negative effects on both (all) competing species (but see the following text). As discussed in Chapter 6, competition among individuals of a given population represents a major negative feedback mechanism for regulation of population size. Similarly, competition among species represents a major mechanism for regulation of the total abundance of multiple-species populations. As the total density of all individuals of competing species increases, each individual has access to a decreasing share of the resource(s). If the competition is asymmetrical, the superior species may com-

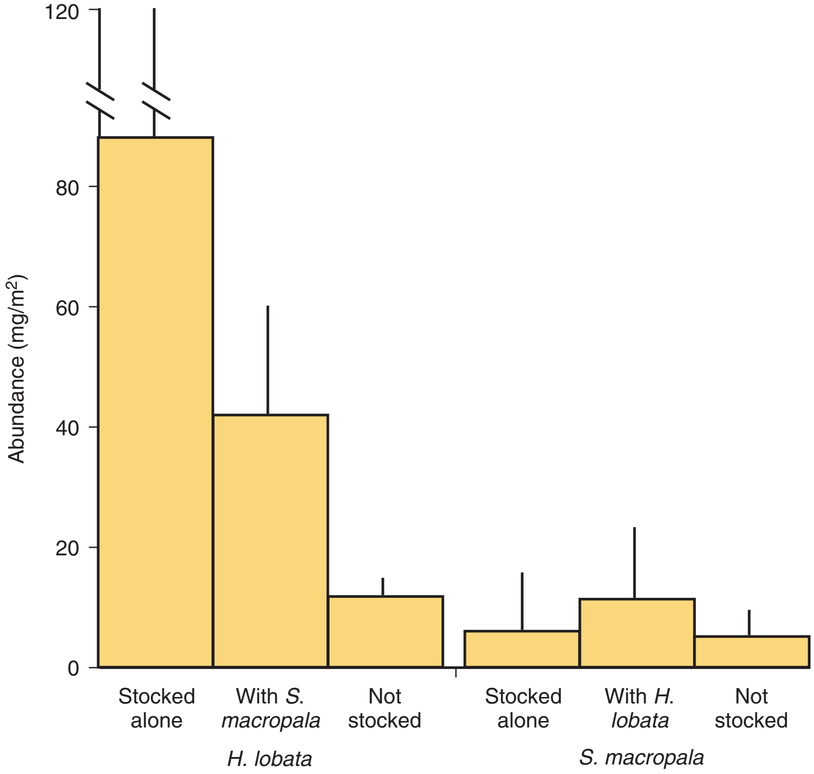


FIG. 8.2 Results of competition between two waterboatmen species, *Hesperocorixa lobata* and *Sigara macropala,* in 1.46 m^2 enclosures in a 1.2-ha pond. Enclosures were stocked in June with adult *H. lobata* or *S. macropala,* or both, and final abundance was measured after 2 months. Waterboatmen in unstocked enclosures provided a measure of colonization. Vertical bars represent 1 S. D. N = 4–8. Data from Istock (1973).

petitively suppress other species, leading over sufficient time to *competitive exclusion* (Denno *et al.* 1995, Park 1948, D. Strong *et al.* 1984). However, Denno *et al.* (1995) found evidence of competitive exclusion in <10% of the competitive interactions they reviewed. Competitive exclusion normally may be prevented by various factors that limit complete preemption of resources by any species. For example, predators that curb population growth of the most abundant competing species can reduce its ability to competitively exclude other species (R. Paine 1966, 1969a, b).

Interspecific competition can take different forms and have different possible outcomes. *Exploitation competition* occurs when all individuals of the competing species have equal access to the resource. A species that can find or exploit a resource more quickly, develop or reproduce more rapidly, or increase its efficiency of resource utilization will be favored under such circumstances. *Interference competition* involves preemptive use, and often defense of, a resource that allows a more aggressive species to increase its access to, and share of, the resource, to the detriment of other species.

Many species avoid resources that have been marked or exploited previously, thereby losing access. It is interesting that males of territorial species usually compete with conspecific males for mates and often do not attack males of other species that also compete for food resources. Foraging ants may attack other predators and preempt prey resources. For example, Halaj *et al.* (1997) reported that exclusion of foraging ants in young conifer plantations increased abundances of arboreal spiders >1.5-fold. Gordon and Kulig (1996) reported that foragers of the harvester ant, *Pogonomyrmex barbatus,* often encounter foragers from neighboring colonies, but relatively few encounters (about 10%) involved fighting, and fewer (21% of fights) resulted in death of any of the participants. Nevertheless, colonies were spaced at distances that indicated competition. Gordon and Kulig (1996) suggested that exploitative competition among ants foraging for resources in the same area may be more costly than is interference competition. Because competition can be costly, in terms of lost resources, time, or energy expended in defending resources (see Chapter 4), evolution should favor strategies that reduce competition. Hence, species competing for a resource might be expected to minimize their use of the contested portion and maximize use of the noncontested portions. This results in partitioning of resource use, a strategy referred to as *niche partitioning.* Over evolutionary time, sufficiently consistent partitioning might become fixed as part of the species' adaptive strategies, and the species would no longer respond to changes in the abundance of the former competitor(s). In such cases, competition is not evident, although niche partitioning may be evidence of competition in the past (Connell 1980). Congeners also usually partition a niche as a result of specialization and divergence into unexploited niches or portions of niches, not necessarily as a result of interspecific competition (Fox and Morrow 1981).

Niche partitioning is observed commonly in natural communities. Species competing for habitat, food resources, or oviposition sites tend to partition thermal gradients, time of day, host species, host size classes, etc. Several examples are noteworthy.

Granivorous ants and rodents frequently partition available seed resources. Ants specialize on smaller seeds and rodents specialize on larger seeds when the two compete. J. Brown *et al.* (1979) reported that both ants and rodents increased in abundance in the short term when the other taxon was removed experimentally. However, Davidson *et al.* (1984) found that ant populations in rodent-removal plots declined gradually but significantly after about 2 years. Rodent populations did not decline over time in ant-removal plots. These results reflected a gradual displacement of small-seeded plants (on which ants specialize) by large-seeded plants (on which rodents specialize) in the absence of rodents. Ant removal led to higher densities of small-seeded species, but these species could not displace large-seeded plants.

Predators frequently partition resources on the basis of prey size. Predators must balance the higher resource gain against the greater energy expenditure (for capture and processing) of larger prey (e.g., Ernsting and van der Werf 1988). Generally, predators should select the largest prey that can be handled efficiently (Holling 1965, Mark and Olesen 1996), but prey size preference also depends on hunger level and prey abundance (Ernsting and van der Werf 1988) (see later in this chapter).

Most bark beetle (Scolytidae) species can colonize extensive portions of dead or dying trees when other species are absent. However, given the relative scarcity of dead or dying trees and the narrow window of opportunity for colonization (the first year after tree death), these insects are adapted to finding such trees rapidly (see Chapter 3) and usually several species co-occur in suitable trees. Under these circumstances, the beetle species tend to partition the subcortical resource on the basis of beetle size because each species shows the highest survival in phloem that is thick enough to accommodate growing larvae and because larger species are capable of repulsing smaller species (e.g., Flamm *et al.* 1993). Therefore, the largest species usually occur around the base of the tree, and progressively smaller species occupy successively higher portions of the bole, with the smallest species colonizing the upper bole and branches. However, other competitors, such as wood-boring cerambycids and buprestids, often excavate through bark beetle mines, feeding on bark beetle larvae and reducing bark beetle survival (see Fig. 8.1) (Coulson *et al.* 1980, Dodds *et al.* 2001).

Many competing species partition resource use in time. Partitioning may be by time of day (e.g., nocturnal versus diurnal Lepidoptera [Schultz 1983] and nocturnal bat and amphibian versus diurnal bird and lizard predators [Reagan *et al.* 1996]) or by season (e.g., asynchronous occurrence of 12 species of water-boatmen [Heteroptera: Corixidae], which breed at different times [Istock 1973]). However, temporal partitioning does not preclude competition through preemptive use of resources or induced host defenses (see later in this chapter).

In addition to niche partitioning, other factors also may obscure or prevent competition. Resource turnover in frequently disturbed ecosystems may prevent species saturation on available resources and prevent competition. Similarly, spatial patchiness in resource availability may hinder resource discovery and prevent species from reaching abundances at which they would compete. Finally, other interactions, such as predation, can maintain populations below sizes at which competition would occur (R. Paine 1966, 1969a, b; see later in this chapter).

Competition has proved to be rather easily modeled (see Chapter 6). The Lotka-Volterra equation generalized for n competitors is as follows:

$$N_{i(t+1)} = N_{it} + r_i N_{it}\left(K - N_{it} - \sum_{j>1}^{n} \alpha_{ij} N_{jt}\right)\Big/ K \qquad (8.1)$$

where N_i and N_j are species abundances, and α_{ij} represents the per capita effect of N_j on the growth of N_i and varies for different species. For instance, species j might have a greater negative effect on species i than species i has on species j (i.e., asymmetrical competition).

Istock (1977) evaluated the validity of the Lotka-Volterra equations for co-occurring species of waterboatmen, *H. lobata* (species 1) and *S. macropala* (species 2), in experimental exclosures (see Fig. 8.2). He calculated the competition coefficients, α_{12} and α_{21}, as follows:

$$\alpha_{12} = (K_1 - N_1)N_2 = 3.67 \quad \text{and} \quad \alpha_{21} = (K_2 - N_2)N_1 = -0.16 \qquad (8.2)$$

The intercepts of the zero isocline ($dN/dt = 0$) for *H. lobata* were $K_1 = 88$ and $K_1/\alpha_{12} = 24$; the intercepts for *S. macropala* were $K_2 = 6$ and $K_2/\alpha_{21} = -38$. The negative K_2/α_{21} and position of the zero isocline for *S. macropala* indicate that the competition is asymmetrical, consistent with the observation that *S. macropala* population growth was not affected significantly by the interaction (see Fig. 8.2). Although niche partitioning by these two species was not clearly identified, the equations correctly predicted the observed coexistence.

B. Predation

Predation has been defined in various ways, as a general process of feeding on other (prey) organisms (e.g., May 1981) or as a more specific process of killing and consuming prey (e.g., Price 1997). Parasitism (and the related parasitoidism), the consumption of tissues in a living host, may or may not be included (e.g., Price 1997). Both predation and parasitism generally are considered to have positive effects for the predator or parasite but negative effects for the prey. In this section, predation is treated as the relatively opportunistic capture of multiple prey during a predator's lifetime. The following section will address the more specific parasite–host interactions.

Although usually considered in the sense of an animal killing and eating other animals (Fig. 8.3), predation applies equally well to carnivorous plants that kill and consume insect prey and to herbivores that kill and consume plant prey, especially those that feed on seeds and seedlings. Predator–prey and herbivore–plant interactions represent similar foraging strategies and are affected by similar factors (prey density and defensive strategy, predator ability to detect and orient toward various cues, etc.; see Chapter 3).

Insects, and related arthropods, represent major predators in terrestrial and aquatic ecosystems. The importance of many arthropods as predators of insects

FIG. 8.3 Predation: syrphid larva preying on a conifer aphid, *Cinara* sp., on Douglas fir.

has been demonstrated widely through biological control programs and experimental studies (e.g., Price 1997, D. Strong *et al.* 1984, van den Bosch *et al.* 1982, Van Driesche and Bellows 1996). However, many arthropods prey on vertebrates as well. Predaceous aquatic dragonfly larvae, water bugs, and beetles include fish and amphibians as prey. Terrestrial ants, spiders, and centipedes often kill and consume amphibians, reptiles, and nestling birds (e.g., C. Allen *et al.* 2004, Reagan *et al.* 1996).

Insects also represent important predators of plants or seeds. Some bark beetles might be considered to be predators to the extent that they kill multiple trees. Seed bugs (Heteroptera), weevils (Coleoptera), and ants (Hymenoptera) are effective seed predators, often kill seedlings, and may be capable of preventing plant reproduction under some conditions (e.g., Davidson *et al.* 1984, Turgeon *et al.* 1994, see Chapter 13).

Insects are an important food source for a variety of other organisms. Carnivorous plants generally are associated with nitrogen-poor habitats and depend on insects for adequate nitrogen (Juniper *et al.* 1989, Krafft and Handel 1991). A variety of mechanisms for entrapment of insects has evolved among carnivorous plants, including water-filled pitchers (pitcher plants), triggered changes in turgor pressure that alter the shape of capture organs (flytraps and bladderworts), and sticky hairs (e.g., sundews). Some carnivorous plants show conspicuous ultraviolet (UV) patterns that attract insect prey (Joel *et al.* 1985), similar to floral attraction of some pollinators (see Chapter 13). Insects also are prey for other arthropods (e.g., predaceous insects, spiders, mites) and vertebrates. Many fish, amphibian, reptile, bird, and mammal taxa feed largely or exclusively on insects (e.g., Dial and Roughgarden 1995, Gardner and Thompson 1998, Tinbergen 1960). Aquatic and terrestrial insects provide the food resource for major freshwater fisheries, including salmonids (Cloe and Garman 1996, Wipfli 1997).

Predation has been widely viewed as a primary means of controlling prey population density. Appreciation for this lies at the heart of predator-control policies designed to increase abundances of commercial or game species by alleviating population control by predators. However, mass starvation and declining genetic quality of populations protected from nonhuman predators have demonstrated the importance of predation to maintenance of prey population vigor, or genetic structure, through selective predation on old, injured, or diseased individuals. As a result of these changing perceptions, predator reintroduction programs are being implemented in some regions. At the same time, recognition of the important role of entomophagous species in controlling populations of insect pests has justified augmentation of predator abundances, often through introduction of exotic species, for biological control purposes (van den Bosch *et al.* 1982, Van Driesche and Bellows 1996). As discussed in Chapter 6, the relative importance of predation to population regulation, compared to other regulatory factors, has been a topic of considerable discussion.

Just as co-evolution between competing species has favored niche partitioning for more efficient resource use, co-evolution between predator and prey has produced a variety of defensive strategies balanced against predator foraging strategies. Selection favors prey that can avoid or defend against predators and favors predators that can efficiently acquire suitable prey. Prey defenses include speed; predator detection and alarm mechanisms; spines or horns; chemical defenses; cryptic, aposematic, disruptive, or deceptive coloration; and behaviors (such as aggregation or warning displays) that enhance these defenses (e.g., Conner *et al.* 2000, Jabłoński 1999, Sillén-Tullberg 1985; see Chapter 4). Prey attributes that increase the energy cost of capture will restrict the number of predators able to exploit that prey.

Predators exhibit a number of attributes that increase their efficiency in immobilizing and acquiring prey, including larger size; detection of cues that indicate vulnerable prey; speed; claws or sharp mouthparts; venoms; and behaviors (such as ambush, flushing, or attacking the most vulnerable body parts) that compensate for or circumvent prey defenses (Jabłoński 1999, Galatowitsch and Mumme 2004, Mumme 2002), and reduce the effort necessary to capture the prey. For example, a carabid beetle, *Promecognathus laevissimus,* straddles its prey, polydesmid millipedes, and quickly moves toward the head. It then pierces the neck and severs the ventral nerve cord with its mandibles, thereby paralyzing its prey and circumventing its cyanide spray defense (G. Parsons *et al.* 1991).

Predators are relatively opportunistic with respect to prey taxa, compared to parasites, although prey frequently are selected on the basis of factors determining foraging efficiency. For example, chemical defenses of prey affect attractiveness to nonadapted predators (e.g., Bowers and Puttick 1988, Stamp *et al.*

1997, Traugott and Stamp 1996). Prey size affects the resource gained per foraging effort expended. Predators generally should select prey sizes within a range that provides sufficient energy and nutrient rewards to balance the cost of capture (Ernsting and van der Werf 1988, Iwasaki 1990, 1991, Richter 1990, Streams 1994, Tinbergen 1960). Within these constraints, foraging predators should attack suitable prey species in proportion to their probability of encounter (i.e., more abundant prey types are encountered more frequently than are less abundant prey types; e.g., Tinbergen 1960).

Predators exhibit both functional (behavioral) and numeric responses to prey density. The functional response reflects predator hunger, handling time required for individual prey, ability to discover prey, handling efficiency resulting from learning, etc. (Holling 1959, 1965, Tinbergen 1960). For many invertebrate predators, the percentage of prey captured is a negative binomial function of prey density, Holling's (1959) type 2 functional response. The ability of type 2 predators to respond individually to increased prey density is limited by their ability to capture and consume individual prey. Vertebrates, and some invertebrates, are capable of increasing their efficiency of prey discovery (e.g., through development of a search image that enhances recognition of appropriate prey; Tinbergen 1960) and prey processing time through learning, up to a point. The percentage of prey captured initially increases as the predator learns to find and handle prey more quickly but eventually approaches a peak and subsequently declines as discovery and handling time reach maximum efficiency, Holling's (1959) type 3 functional response. The type 3 functional response is better able, than the type 2 response, to regulate prey population size(s) because of its capacity to increase the percentage of prey captured as prey density increases, at least initially.

Various factors affect the relationship between prey density and proportion of prey captured. The rate of prey capture tends to decline as a result of learned avoidance of distasteful prey, and the maximum rate of prey capture depends on how quickly predators become satiated and on the relative abundances of palatable and unpalatable prey (Holling 1965). Some insect species, such as the periodical cicadas, apparently exploit the functional responses of their major predators by appearing en masse for brief periods following long periods of inaccessibility. Predator satiation maximizes the success of such mass emergence and mating aggregations (K. Williams and Simon 1995). Palatable species experience greater predation when associated with less palatable species than when associated with equally or more palatable species (Holling 1965).

In addition to these functional responses, predator growth rate and density tend to increase with prey density. Fox and Murdoch (1978) reported that growth rate and size at molt of the predaceous heteropteran, *Notonecta hoffmanni,* increased with prey density in laboratory aquaria. Numeric response reflects predator orientation toward, and longer residence in, areas of high prey density and subsequent reproduction in response to food availability. However, increased predator density also may increase competition, and conflict, among predators. The combination of type 3 functional response and numeric response (total response) makes predators effective in cropping abundant prey and maintaining relatively stable populations of various prey species. However, the tendency to become satiated and to reproduce more slowly than their prey limits the ability of predators to regulate irruptive prey populations released from other controlling factors.

The importance of predator–prey interactions to population and community dynamics has generated considerable interest in modeling this interaction. The effect of a predator on a prey population was first incorporated into the logistic model by Lotka (1925) and Volterra (1926). As described in equation 6.11, their model for prey population growth was as follows:

$$N_{1(t+1)} = N_{1t} + r_1 N_{1t} - p_1 N_{1t} N_{2t}$$

where N_2 is the population density of the predator and p_1 is a predation constant. Lotka and Volterra modeled the corresponding predator population as follows:

$$N_{2(t+1)} = N_{2t} + p_2 N_{1t} N_{2t} - d_2 N_{2t} \tag{8.3}$$

where p_2 is a predation constant and d_2 is per capita mortality of the predator population. The Lotka-Volterra equations describe prey and predator populations oscillating cyclically and out of phase over time. Small changes in parameter values lead to extinction of one or both populations after several oscillations of increasing amplitude.

Pianka (1974) proposed modifications of the Lotka-Volterra competition and predator–prey models to incorporate competition among prey and among predators for prey. Equation 6.12 represents the prey population:

$$N_{1(t+1)} = N_{1t} + r_1 N_{1t} - r_1 N_{1t}^{\,2} / K_1 - r_1 N_{1t} \alpha_{12} N_{2t} / K_1$$

where α_{12} is the per capita effect of the predator on the prey population. The corresponding model for the predator population is as follows

$$N_{2(t+1)} = N_{2t} + \alpha_{21} N_{1t} N_{2t} - \beta_2 N_{2t}^{\,2} / N_{1t} \tag{8.4}$$

where α_{21} is the negative effect of predation on the prey population and β_2 incorporates the predator's carrying capacity as a function of prey density (Pianka 1974). This refinement provides for competitive inhibition of the predator population as a function of the relative densities of predator and prey. The predator–prey equations have been modified further to account for variable predator and prey densities (Berlow *et al.* 1999), predator and prey distributions (see Begon and Mortimer 1981), and functional responses and competition among predators for individual prey (Holling 1959, 1966). Other models have been developed primarily for parasitoid–prey interactions (see later in this chapter).

Current modeling approaches have focused on paired predator and prey. Real communities are composed of multiple predator species exploiting multiple prey species, resulting in complex interactions (Fig. 8.4). Furthermore, predator effects on prey are more complex than mortality to prey. Predators also affect the distribution and behavior of prey populations. For example, Cronin *et al.* (2004) found that web-building spiders, at high densities, were more likely to affect planthoppers, *Prokelisia crocea,* through induced emigration than through direct

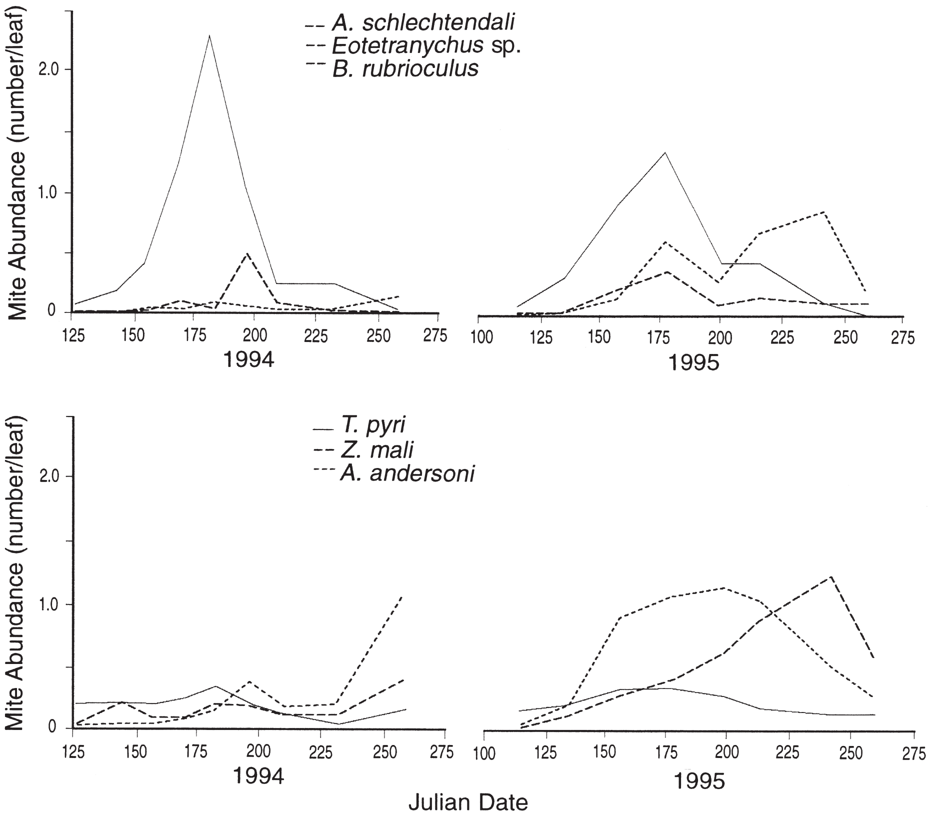


FIG. 8.4 Densities of three phytophagous mites, *Aculus schlechtendali, Bryobia rubrioculus,* and *Eotetranychus* sp. (prey), and three predaceous mites, *Amblyseius andersoni, Typhlodromus pyri,* and *Zetzellia mali,* in untreated apple plots (N = 2) during 1994 and 1995. Data from Croft and Slone (1997).

mortality. Johansson (1993) reported that immature damselflies, *Coenagrion hastulatum,* increased avoidance behavior and reduced foraging behavior when immature dragonfly, *Aeshna juncea,* predators were introduced into experimental aquaria.

C. Symbiosis

Symbiosis involves an intimate association between two unrelated species. Three types of interactions are considered symbiotic, although the term often has been used as a synonym for only one of these, mutualism. Parasitism describes interactions in which the symbiont derives a benefit at the expense of the host, as in predation. Commensalism occurs when the symbiont derives a benefit without significantly affecting its partner. Mutualism involves both partners benefiting from the interaction. Insects have provided some of the most interesting examples of symbiosis.

1. Parasitism

Parasitism affects the host (prey) population in ways that are similar to predation and can be described using predation models. However, whereas predation involves multiple prey killed and consumed during a predator's lifetime, parasites feed on living prey. Parasitoidism is unique to insects, especially flies and wasps, and combines attributes of both predation and parasitism. The adult parasitoid usually deposits eggs or larvae on, in, or near multiple hosts, and the larvae subsequently feed on their living host and eventually kill it (Fig. 8.5). Parasites must be adapted to long periods of exposure to the defenses of a living host (see Chapter 3). Therefore, parasitic interactions tend to be relatively specific associations between co-evolved parasites and their particular host species and may involve modification of host morphology, physiology, or behavior to benefit parasite development or transmission. Because of this specificity, parasites and parasitoids tend to be more effective than predators in responding to and controlling population irruptions of their hosts and, therefore, have been primary agents in biological control programs (Hochberg 1989). In fact, release from parasites may largely explain the rapid spread of invasive plants and animals (Torchin and Mitchell 2004).

Parasitic interactions can be quite diverse and complex. Parasites can be assigned to several categories (van den Bosch *et al.* 1982). *Ectoparasites* feed externally, by inserting mouthparts into the host (e.g., lice, fleas, mosquitoes, ticks), and *endoparasites* feed internally, within the host's body (e.g., bacteria,

FIG. 8.5 Parasitism: a parasitoid (sarcophagid fly) ovipositing on a host caterpillar at Nanjinshan Long Term Ecological Research Site, Taiwan.

nematodes, bot flies, and wasps). A *primary parasite* develops on or in a nonparasitic host, whereas a *hyperparasite* develops on or in another parasite. Some parasitic species parasitize other members of the same species (*autoparasitism* or *adelphoparasitism*), as is the case for the hymenopteran, *Coccophagus scutellaris.* The female of this species parasitizes scale insects and the male is an obligate hyperparasite of the female (van den Bosch *et al.* 1982). *Superparasitism* refers to more individuals of a parasitoid species occurring in the host than can develop to maturity. *Multiple parasitism* occurs when more than one parasitoid species is present in the host simultaneously. In most cases of superparasitism and multiple parasitism, one dominant individual competitively suppresses the others and develops to maturity. In a special case of multiple parasitism, some parasites preferentially attack hosts parasitized by other species (*cleptoparasitism*). The cleptoparasite is not a hyperparasite but usually kills and consumes the original parasite as well as the host.

Insects are parasitized by a number of organisms, including viruses, bacteria, fungi, protozoa, nematodes, flatworms, mites, and other insects (Hajek and St. Leger 1994, Tanada and Kaya 1993, Tzean *et al.* 1997). Some parasites cause sufficient mortality that they have been exploited as agents of biological control (van den Bosch *et al.* 1982). Epidemics of parasites often are responsible for termination of host outbreaks (Hajek and St. Leger 1994, Hochberg 1989). Parasites also have complex sublethal effects that make their hosts more vulnerable to other mortality factors. For example, Bradley and Altizer (2005) reported that monarch butterflies, *Danaus plexippus,* parasitized by the protozoan, *Ophryocystis elektroscirrha,* lost 50% more body mass per kilometer flown and exhibited 10% slower flight velocity, 14% shorter flight duration, and 19% shorter flight distance, compared to uninfected butterflies. These data, together with much higher infection rates among nonmigrating monarchs (Altizer *et al.* 2000), suggest that long-distance migration of this species may eliminate infected individuals and reduce rates of parasitism.

Some parasites alter the physiology or behavior of their hosts in ways that enhance parasite development or transmission. For example, parasitic nematodes often destroy the host's genital organs, sterilizing the host (Tanada and Kaya 1993). Parasitized insects frequently show prolonged larval development (Tanada and Kaya 1993). Flies, grasshoppers, ants, and other insects infected with fungal parasites often climb to high places where they cling following death, facilitating transmission of wind-blown spores (Tanada and Kaya 1993) (Fig. 8.6).

Insects have evolved various defenses against parasites (see Chapter 3). Ants stop foraging and retreat to nests when parasitoid phorid flies appear (Feener 1981, Mottern *et al.* 2004, Orr *et al.* 2003). Hard integument, hairs and spines, defensive flailing, and antibiotics secreted by metapleural glands prevent attachment or penetration by some parasites (e.g., Hajek and St. Leger 1994, Peakall *et al.* 1987). Ingested or synthesized antibiotics or gut modifications prevent penetration by some ingested parasites (Tallamy *et al.* 1998, Tanada and Kaya 1993). Endocytosis is the infolding of the plasma membrane by a phagocyte engulfing and removing viruses, bacteria, or fungi from the hemocoel. When the foreign

FIG. 8.6 Parasitism: stinkbug infected and killed by a parasitic fungus in Louisiana, United States.

particle is too large to be engulfed by phagocytes, aggregation and adhesion of hemocytes can form a dense covering around the particle, encapsulating and destroying the parasite (Tanada and Kaya 1993). However, some parasitic wasps inoculate the host with a virus that inhibits the encapsulation of their eggs or larvae (Edson *et al.* 1981, Godfray 1994).

Many insects and other arthropods function in the capacity of parasites. Although parasitism generally is associated with animal hosts, most insect herbivores can be viewed as parasites of living plants (Fig. 8.7). Some herbivores, such as sap-suckers, leaf miners, and gall-formers, are analogous to blood-feeding or internal parasites of animals. Virtually all terrestrial arthropods and vertebrates are parasitized by insect or mite species. The majority of insect parasites of animals are wasps, flies, fleas, and lice, but some beetle species also are parasites (e.g., Price 1997). Parasitic wasps are a highly diverse group that differentially parasitize the eggs, juveniles, pupae, or adults of various arthropods. Spider wasps (e.g., tarantula hawks) provision burrows with paralyzed spiders for their parasitic larvae. Flies parasitize a wider variety of hosts. Mosquitoes and other biting flies are important blood-sucking ectoparasites of vertebrates. Oestrid and tachinid flies are important endoparasites of vertebrates and insects. Fleas and lice are ectoparasites of vertebrates. Mites, chiggers, and ticks parasitize a wide variety of hosts.

Insect parasites can significantly reduce growth, survival, reproduction, and movement of their hosts (J. Day *et al.* 2000, Steelman 1976). Biting flies can reduce

FIG. 8.7 Parasitism: a nymphalid caterpillar feeding on cecropia foliage in Puerto Rico.

growth and survival of wildlife species through irritation, blood loss, or both (J. Day *et al.* 2000). DeRouen *et al.* (2003) reported that horn fly control resulted in significantly reduced numbers of horn flies on treated cattle (14% of horn fly numbers on untreated cattle) and a significant 14% increase in cattle weight but no effect on reproductive rate. However, Sanson *et al.* (2003) found that control of horn flies, *Haematobia irritans,* resulted in significantly reduced horn fly abundance but was associated with significantly increased weight of cattle in only 1 of 3 years of study. Other studies of the effects of arthropod parasites of livestock also have shown that direct effects of parasites on host productivity may be more variable. Amoo *et al.* (1993) reported that a range of acaricide treatments to reduce tick, primarily *Amblyomma gemma,* parasitism of cattle had little effect on growth, reproduction, or milk production in the most and least intensive treatments. Although tick abundance in the most intensive treatment was only 14% of the abundance in the least intensive treatment, the lowest weight gain was observed in the most intensive treatment group, suggesting that reduced exposure to ticks may have prevented acquisition of resistance to tick-borne diseases.

Many arthropod parasites also vector animal pathogens, including agents of malaria (*Plasmodium malariae*), bubonic plague (*Yersinia pestis*), and encephalitis (arboviruses) (Edman 2000). Some of these diseases cause substantial mortality in human, livestock, and wildlife populations, especially when contracted by nonadapted hosts (Amoo *et al.* 1993, Marra *et al.* 2004, Stapp *et al.* 2004, Steelman 1976, Zhou *et al.* 2002). Human population dynamics, including invasive military campaigns, have been substantially shaped by insect-vectored diseases (Diamond 1999, R. Peterson 1995).

Generally, parasitoids attack only other arthropods, but a sarcophagid fly, *Anolisomyia rufianalis,* is a parasitoid of *Anolis* lizards in Puerto Rico. Dial and Roughgarden (1996) found a slightly higher rate of parasitism of *Anolis evermanni,* compared to *Anolis stratulus.* They suggested that this difference in parasitism may be the result of black spots on the lateral abdomen of *A. stratulus* that resemble the small holes made by emerging parasites. Host-seeking flies may tend to avoid lizards showing signs of prior parasitism.

Nicholson and Bailey (1935) proposed a model of parasitoid–prey interactions that assumed that prey are dispersed regularly in a homogeneous environment, that parasitoids search randomly within a constant area of discovery, and that the ease of prey discovery and parasitoid oviposition do not vary with prey density. The number of prey in the next generation (u_s) was calculated as follows:

$$pa = \log_e(u_i/u_s) \tag{8.5}$$

where p = parasitoid population density, a = area of discovery, and u_i = host density in the current generation.

Hassell and Varley (1969) showed that the area of discovery (a) is not constant for real parasitoids. Rather, log a is linearly related to parasitoid density (p) as follows:

$$\log a = \log Q - (m \log p) \tag{8.6}$$

where Q is a quest constant and m is a mutual interference constant. Hassell and Varley (1969) modified the Nicholson-Bailey model to incorporate density limitation (Q/p^m). By substitution,

$$pa = \log_e(u_i/u_s) = Qp^{1-m} \tag{8.7}$$

As m approaches Q, model predictions approach those of the Nicholson-Bailey model.

2. Commensalism

Commensalism benefits the symbiont without significantly affecting the host. This is a relatively rare type of interaction because few hosts can be considered to be completely unaffected by their symbionts. Epiphytes, plants that benefit by using their hosts for aerial support but gain their resources from the atmosphere, and cattle egrets, which eat insects flushed by grazing cattle, are well-known examples of commensalism. However, epiphytes may capture and provide nutrients to the host (a benefit) and increase the likelihood that overweight branches will break during high winds (a detriment). Some interactions involving insects may be largely commensal.

Phoretic or vector interactions (see Fig. 2.15) benefit the hitchhiker or pathogen, especially when both partners have the same destination, and may have little or no effect on the host. However, hosts can become overburdened when the symbionts are numerous, inhibiting dispersal, resource acquisition, or escape. In some cases, the phoretic partners may be mutualists, with predaceous hitchhikers reducing competition or parasitism for their host at their destination

(Kinn 1980). Examples of commensalism often may be seen to exemplify other interaction types as additional information becomes available.

A number of insect and other arthropod species function as nest commensals in ant or termite colonies. Such species are called myrmecophiles or termitophiles, respectively. These symbionts gain shelter, and often detrital food, from their host colonies with little, if any, effect on their hosts. This relationship is distinguished from interactions involving species that intercept host food (through trophallaxis) and, therefore, function as colony parasites. Some vertebrate species also are commensals of termite castles in the tropics. These termite nests may reach several meters in height and diameter and provide critical shelter for reptile, bird, and mammal species in tropical savannas (see Chapter 14).

Bark beetle galleries provide habitat and resources for a variety of invertebrate and microbial commensals, most of which have little or no effect on the bark beetles (e.g., Stephen *et al.* 1993). Many of the invertebrate species are fungivores or detritivores that depend on penetration of the bark by bark beetles to exploit resources provided by the microbial decay of wood (Fig. 8.8).

3. *Mutualism*

Mutualistic interactions benefit both partners (positive effects on each) and therefore represent cooperative or mutually exploitative relationships. One member of a mutualism provides a resource that is exploited by the other (the symbiont). The symbiont, in turn, unintentionally provides a service to its host.

FIG. 8.8 Commensalism: an unidentified mite in an ambrosia beetle, *Trypodendron lineatum*, mine in Douglas-fir. A variety of predaceous and detritivorous mites exploit resources in bark and ambrosia beetle mines.

For example, plants expend resources to attract pollinators, ants (for defense), or mycorrhizal fungi, which perform a service to the plant in the process of exploiting plant resources. Similarly, bark beetles provide nourishment to their symbiotic microorganisms that improve resource suitability for their host as a consequence of being transported to new resources (see later in this section). Gut symbionts of many insects, and other animals, provide nourishment as a consequence of exploiting resources in the host gut. Some mutualisms require less sacrifice of resources by either member of the pair. For example, aphids attract ants to their waste product, honeydew, and benefit from the protection the ants provide.

Mutualisms have received considerable attention, and much research has focused on examples such as pollination (see Chapter 13), ant–plant and mycorrhizae–plant interactions, and other conspicuous mutualisms. Nevertheless, Price (1997) argued that ecologists have failed to appreciate mutualism as equal in importance to predation and competition, at least in temperate communities, reflecting a perception, based on early models, that mutualism is less stable than competition or predation (e.g., Goh 1979, May 1981, M. Williamson 1972). However, as Goh (1979) noted, such models did not appear to reflect the widespread occurrence of mutualism in ecosystems. As a cooperative relationship, mutualism can contribute greatly to the presence and ecological function of the partners, but the extent to which such positive feedback stabilizes or destabilizes interacting species populations remains a topic of discussion.

Mutualistic interactions tend to be relatively specific associations between co-evolved partners and often involve modification of host morphology, physiology, or behavior to provide habitat or food resources for the symbiont. In return, the symbiont provides necessary resources or protection from competitors or predators. Although the classic examples of mutualism often involve mutually dependent (obligate) partners (i.e., disappearance of one leads to demise of the other) some mutualists are less tightly coupled. However, Janzen and Martin (1982) suggested that some mutualisms might reflect substitution for an extinct co-evolved symbiont by an extant symbiont, by virtue of similar attributes (see Chapter 13). To some degree, herbivores on plants often may function as mutualists, pruning and permitting reallocation of resources to more productive plant parts in return for their resources. Many insect species engage in mutualistic interactions with other organisms, including plants, microorganisms, and other insects.

Among the best-known mutualisms are those involving pollinator and ant associations with plants (Feinsinger 1983, Huxley and Cutler 1991, Jolivet 1996). The variety of obligate relationships between pollinators and their floral hosts in the tropics perhaps has contributed to the perception that mutualism is more widespread and important in the tropics. As discussed in Chapter 13, the prevalence of obligate mutualisms between plants and pollinators in the tropics, compared to temperate regions, largely reflects the high diversity of plant species, which precludes wind pollination between nearest neighbors. Sparsely distributed or understory plants in temperate regions also tend to have mutualistic association with pollinators. Other mutualistic associations (e.g., insect–microbial association; see later in this section) may be more prominent in temperate than in tropical regions. Many plants provide nest sites or shelters (domatia) (e.g., hollow stems or pilose vein axils) for ants or predaceous mites that protect the plant from herbivores (O'Dowd and Willson 1991). Other plant species provide extrafloral nectaries rich in amino acids and lipids that attract ants (e.g., Dreisig 1988, Jolivet 1996, Oliveira and Brandâo 1991, Rickson 1971, Schupp and Feener 1991, Tilman 1978). In addition to defense, plants also may acquire nitrogen or other nutrients from the ants (Fischer *et al.* 2003).

Clarke and Kitching (1995) discovered an unusual example of a mutualistic interaction between an ant and a carnivorous pitcher plant in Borneo. The ant, *Camponotus* sp., nests in hollow tendrils of the plant, *Nepenthes bicalcarata,* and is capable of swimming in pitcher plant fluid, where it feeds on large prey items caught in the pitcher. Through ant-removal experiments, Clarke and Kitching found that accumulation of large prey (but not small prey) in ant-free pitchers led to putrefaction of the pitcher contents and disruption of prey digestion by the plant. By removing large prey, the ants prevent putrefaction and accumulation of ammonia.

Seed-feeding ants often benefit plants by assisting dispersal of unconsumed seeds. This mutualism is exemplified by myrmecochorous plants that provide a nutritive body (elaiosome) attached to the seed to attract ants. The elaiosome usually is rich in lipids (Gorb and Gorb 2003, Jolivet 1996). The likelihood that a seed will be discarded in or near an ant nest following removal of the elaiosome increases with elaiosome size, perhaps reflecting increasing use by seed-disperser, rather than seed-predator, species with increasing elaiosome size (Gorb and Gorb 2003, Mark and Olesen 1996, Westoby *et al.* 1991). The plants benefit primarily through seed dispersal by ants (Horvitz and Schemske 1986, Ohkawara *et al.* 1996), not necessarily from seed relocation to more nutrient-rich microsites (Horvitz and Schemske 1986, Westoby *et al.* 1991; see Chapter 13). This interaction has been implicated in the rapid invasion of new habitats by myrmecochorous species (J. M. B. Smith 1989).

Gressitt *et al.* (1965, 1968) reported that large phytophagous weevils (Coleoptera: Curculionidae) in the genera *Gymnopholus* and *Pantorhytes* host diverse communities of cryptogamic plants, including fungi, algae, lichens, liverworts, and mosses, on their backs. These weevils have specialized scales or hairs and produce a thick waxy secretion from glands around depressions in the elytra that appear to foster the growth of these symbionts. In turn, the weevils benefit from the camouflage provided by this growth and, possibly, from chemical protection. Predation on these weevils appears to be rare.

Insects exhibit a wide range of mutualistic interactions with microorganisms. Parasitoid wasps inoculate their host with a virus that prevents cellular encapsulation of the parasitoid larva (Edson *et al.* 1981, Godfray 1994; see Chapter 3). Intestinal bacteria may synthesize some of the pheromones used by bark beetles to attract mates (Byers and Wood 1981). Most aphids harbor mutualistic bacteria or yeasts in specialized organs (bacteriomes or mycetomes) that appear to provide amino acids, vitamins, or proteins necessary for aphid development and reproduction (Baumann *et al.* 1995). Experimental elimination of the microbes results in aphid sterility, reduced weight, and reduced survival. Many homopterans vector plant pathogens and may benefit from changes in host condition induced by infection (Kluth *et al.* 2002). Leaf-cutting ants, *Atta* spp. and *Acromyrmex* spp., cultivate fungus gardens that provide food for the ants (e.g., Currie 2001, Weber 1966).

Virtually all wood-feeding species interact mutualistically with some cellulose-digesting microorganisms. Ambrosia beetles (Scolytidae and Platypodidiae) are the only means of transport for ambrosia (mold) fungi, carrying hyphae in specialized invaginations of the cuticle (mycangia) that secrete lipids for fungal nourishment, and require the nutrition provided by the fungus. The adult beetles carefully cultivate fungal gardens in their galleries, removing competing fungi. Their offspring feed exclusively on the fungus, which derives its resources from the wood surrounding the gallery, and collect and transport fungal hyphae when they disperse (Batra 1966, French and Roeper 1972).

Siricid wasps also are the only means of dispersal for associated *Amylostereum* (decay) fungi, and larvae die in the absence of the fungus (Morgan 1968). The adult female wasp collects fungal hyphae from its gallery prior to exiting. The wasp stores and nourishes the fungus in a mycangium at the base of the ovipositor, then introduces the fungus during oviposition in the wood. The fungus decays the wood around the larva that feeds on the fungal mycelium, destroying it in the gut, and passes decayed wood fragments around the body to combine posteriorly with its frass. Phloem-feeding bark beetles transport mycangial fungi and bacteria as well as opportunistic fungi. Ayres *et al.* (2000) reported that mycangial fungi significantly increased nitrogen concentrations in phloem surrounding southern pine beetle, *Dendroctonus frontalis,* larvae, compared to uncolonized phloem. Opportunistic fungi, including blue-stain *Ophiostoma minus,* did not concentrate nitrogen in phloem surrounding larvae, suggesting that the apparent antagonism between this fungus and the bark beetle may reflect failure to enhance phloem nutrient concentrations (see later in this chapter). Termites similarly depend on mutualistic bacteria or protozoa in their guts for digestion of cellulose (Breznak and Brune 1994).

Many mutualistic interactions involve insects and other arthropods. A well-known example is the mutualism between honeydew-producing Homoptera and ants (Fig. 8.9). Homoptera excrete much of the carbohydrate solution (honeydew) that composes plant sap so as to concentrate sufficient nutrients (see Chapter 3). Aphid species are particularly important honeydew producers. A variety of species are tended by ants that harvest this carbohydrate resource and protect the aphids from predators and parasites (Bristow 1991, Dixon 1985, Dreisig 1988). This mutualism involves only about 25% of aphid species and varies in its strength and benefits, perhaps reflecting plant chemical influences or the relative costs of defending aphid colonies (Bristow 1991). Ant species show different preferences among aphid species, and the efficiency of protection often varies inversely with aphid and ant densities (Bristow 1991, Cushman and Addicott 1991, Dreisig 1988).

Dung beetles (Scarabaeidae) and bark beetles often have mutualistic association with phoretic, predaceous mites. The beetles are the only means of

FIG. 8.9 Mutualism: ant tending honeydew-producing aphids in Georgia, United States. Photo courtesy of S. D. Senter.

long-distance transport for the mites, and the mites feed on the competitors or parasites of their hosts (Kinn 1980, Krantz and Mellott 1972).

Although mutualism usually is viewed from the perspective of mutual benefits, this interaction also can be viewed as mutual exploitation or manipulation. The structures and resources necessary to maintain the mutualism represent costs to the organisms involved. For example, the provision of domatia or extrafloral nectaries by ant-protected plants represents a cost in terms of energy and nutrient resources that otherwise could be allocated to growth and reproduction. Ants may provide nitrogen or other nutrients, as well as defense, for their hosts (Fischer *et al.* 2003). Therefore, plants may lose ant-related traits when the benefit from the ants is removed (Rickson 1977).

Models of mutualistic interactions have lagged behind models for competitive or predator–prey interactions, largely because of the difficulty of simultaneously incorporating negative (density-limiting) and positive (density-increasing) feedback. The Lotka-Volterra equations may be inadequate for extension to mutualism because they lead to unbounded exponential growth of both populations (May 1981, but see Goh 1979). May (1981) asserted that minimally realistic models for mutualists must allow for saturation in the magnitude of at least one of the reciprocal benefits, leading to a stable equilibrium point, with one (most often both) of the two equilibrium populations being larger than that sustained in the absence of the mutualistic interaction. However, recovery from perturbations to this equilibrium may take longer than in the absence of the mutualistic interaction, leading to instability (May 1981). May (1981) presented a simple model for two mutualistic populations:

$$N_{1(t+1)} = N_{1t} + r_1 N_{1t}[1 - (N_{1t} + \alpha N_2)/K_1] \qquad (8.8)$$

$$N_{2(t+1)} = N_{2t} + r_2 N_{2t}[1 - (N_{2t} + \beta N_1)/K_2] \qquad (8.9)$$

in which the carrying capacity of each population is increased by the presence of the other, with α and β representing the beneficial effect of the partner, $K_1 \rightarrow K_1 + \alpha N_2$, $K_2 \rightarrow K_2 + \beta N_1$ and $\alpha\beta < 1$ to limit uncontrolled growth of the two populations. The larger the product, $\alpha\beta$, the more tightly coupled the mutualists. For obligate mutualists, a threshold effect must be incorporated to represent the demise of either partner if the other becomes rare or absent. May (1981) concluded that mutualisms are stable when both populations are relatively large and increasingly unstable at lower population sizes, with a minimum point for persistence.

Dean (1983) proposed an alternative model that incorporates density dependence as the means by which two mutualists can reach a stable equilibrium. As a basis for this model, Dean developed a model to describe the relationship between population carrying capacity (k_y) and an environmental variable (M) that limits k_y:

$$dk_y/dM = a(K_y - k_y)/K_y \qquad (8.10)$$

where K_y is the maximum value of k_y and the constant a is reduced by a linear function of k_y. This equation can be integrated as follows:

$$k_y = K_y(1 - e^{(-aM+Cy)/Ky}) \qquad (8.11)$$

where C_y is the integration constant. Equation (8.11) describes the isocline where $dY/dt = 0$.

For species Y exploiting a replenishable resource provided by species X, Equation (8.11) can be rewritten as follows:

$$k_y = K_y\left(1 - e^{(-aNx+Cy)/Ky}\right) \qquad (8.12)$$

where N_x is the number of species X. The carrying capacity of species X depends on the value of Y and can be described as follows:

$$k_x = K_x(1 - e^{(-bNy+Cx)/Kx}) \qquad (8.13)$$

where N_y is the number of species Y. Mutualism will be stable when the number of one mutualist (N_y) maintained by a certain number of the other mutualist (N_x) is greater than the N_y necessary to maintain N_x. When this condition is met, both populations grow until density effects limit the population growth of X and Y, so that isoclines defined by Equations (8.12) and (8.13) inevitably intersect at a point of stable equilibrium. Mutualism cannot occur when the isoclines do not intersect and is unstable when the isoclines are tangential. This condition is satisfied when any value of N_x or N_y can be found to satisfy either of the following equations:

$$K_y(1 - e^{(-aN\times Cy)/Ky}) > -(C_x + K_x[\ln(K_x - N_x) - \ln K_x])/b \qquad (8.14)$$

$$K_x(1-e^{(-bNy+Cx)/Kx}) > -(C_y + K_y[\ln(K_y - N_y) - \ln K_y])/a \qquad (8.15)$$

The values of the constants, C_x and C_y, in equations (8.13) and (8.14) indicate the strength of mutualistic interaction. When C_x and $C_y > 0$, the interacting species are facultative mutualists; when C_x and $C_y = 0$, both species are obligate mutualists; when C_x and $C_y < 0$, both species are obligate mutualists and their persistence is determined by threshold densities (Fig. 8.10).

The growth rates of the two mutualists can be described by modified logistic equations as follows:

$$N_{y(t+1)} = N_{y(t)} + (r_y N_{y(t)}[k_y - N_{y(t)}])/k_y \qquad (8.16)$$

$$N_{x(t+1)} = N_{x(t)} + (r_x N_{x(t)}[k_x - N_{x(t)}])/k_x \qquad (8.17)$$

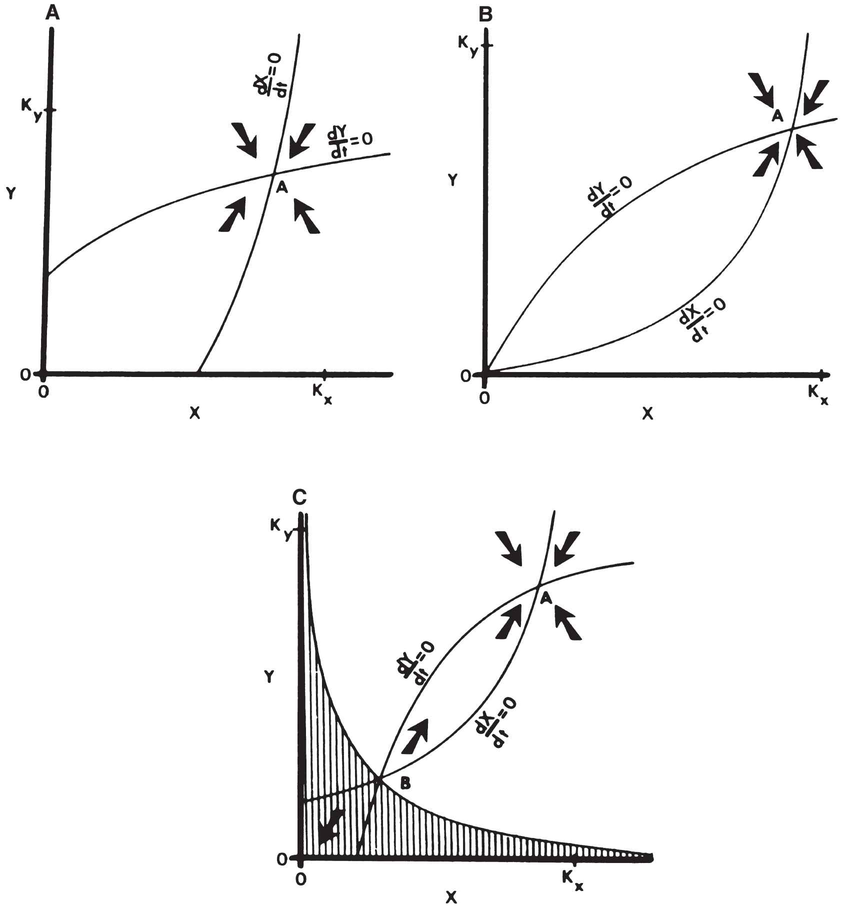


FIG. 8.10 The effect of integration constants in Dean's (1983) model on the form of mutualism (see text for equations) over a range of densities (X and Y) for two interacting species. **A:** When C_x and $C_y > 0$, the interacting species are facultative mutualists; B: when C_x and $C_y = 0$, both species are obligate mutualists; and **C:** when C_x and $C_y < 0$, both species are obligate mutualists and have extinction thresholds at densities of B. Reprinted with permission from the University of Chicago. Please see extended permission list pg 571.

where r_y and r_x are the intrinsic rates of increase for species Y and X, respectively. However, k_y and k_x are not constants but are determined by equations (8.12) and (8.13).

II. FACTORS AFFECTING INTERACTIONS

Multispecies interactions are highly complex. Species can simultaneously compete for space and enhance each other's food acquisition (mutualism), as described by Cardinale *et al.* (2002) for three caddisfly species that in combination increase substrate surface heterogeneity and near-surface velocity and turbulent flow that control food delivery (see later in this section). Two species with overlapping resource requirements could become "competitive mutualists" with respect to a third species that would compete more strongly for the shared resources (Pianka 1981).

The strength, and even type, of interaction can vary over time and space depending on biotic and abiotic conditions (e.g., B. Inouye 2001, Tilman 1978). Interactions can change during life history development or differ between sexes. For example, immature butterflies (caterpillars) are herbivores, but adult butterflies are pollinators. Insects with aquatic immatures are terrestrial as adults. Immature males of the strepsipteran family Myrmecolacidae parasitize ants, whereas immature females parasitize grasshoppers (de Carvalho and Kogan 1991). Herbivores and host plants often interact mutualistically at low herbivore population densities, with the herbivore benefiting from plant resources and the plant benefiting from limited pruning, but the interaction becomes increasingly predatory as herbivory increases and plant condition declines (see Chapter 12).

The strength of an interaction depends on the proximity of the two species, their ability to perceive each other, their relative densities, and their motivation to interact. These factors in turn are affected by abiotic conditions, resource availability, and indirect effects of other species. Modeling interaction strength for prediction of community dynamics has taken a variety of approaches that may be subject to unrecognized biases or to nonlinear or indirect effects (Abrams 2001, Berlow *et al.* 1999).

A. Abiotic Conditions

Relatively few studies have addressed the effects of abiotic conditions on species interactions. J. Chase (1996) experimentally manipulated temperature and solar radiation in experimental plots containing grasshoppers and wolf spiders in a grassland. When temperature and solar radiation were reduced by shading during the morning, grasshopper activity was reduced, but spider activity was unaffected, and spiders reduced grasshopper density. In contrast, grasshopper activity remained high in unshaded plots, and spiders did not reduce grasshopper density. Stamp and Bowers (1990) also noted that temperature affects the interactions between plants, herbivores, and predators.

Hart (1992) studied the relationship between crayfish, their caddisfly (Trichoptera) prey, and the algal food base in a stream ecosystem. He found that crayfish foraging activity was impaired at high flow rates, limiting predation on the caddisfly grazers and altering the algae–herbivore interaction. Kelly *et al.* (2003) reported that exposure of stream communities to UV radiation reduced aquatic grazing and led to increased algal biomass.

Abiotic conditions that affect host growth or defensive capability influence predation or parasitism. Increased exposure to sunlight can increase plant production of defensive compounds and reduce herbivory (Dudt and Shure 1994, Niesenbaum 1992). Light availability to plants may affect their relative investment in toxic compounds versus extrafloral nectaries and domatia to facilitate defense by ants (Davidson and Fisher 1991). Fox *et al.* (1999) reported that drought stress did not affect growth of St. John's wort, *Hypericum perforatum,* in the United Kingdom directly, but it increased plant vulnerability to herbivores. Stamp *et al.* (1997) found that the defensive chemicals sequestered by caterpillars had greater negative effects on a predator at higher temperatures.

Altered atmospheric conditions (e.g., CO_2 enrichment or pollutants) affect interactions (Alstad *et al.* 1982, Arnone *et al.* 1995, V. C. Brown 1995, Heliövaara and Väisänen 1986, 1993, Kinney *et al.* 1997, Roth and Lindroth 1994, Salt *et al.* 1996). For example, Hughes and Bazzaz (1997) reported that elevated CO_2 significantly increased C to N ratio and decreased percentage nitrogen in milkweed, *Asclepias syriaca,* tissues, resulting in lower densities but greater per capita leaf damage by the western flower thrips, *Frankliniella occidentalis.* However, increased plant growth at elevated CO_2 levels more than compensated for leaf damage. Yet Salt *et al.* (1996) reported that elevated CO_2 did not affect the competitive interaction between shoot- and root-feeding aphids. Mondor *et al.* (2004) found that the aphid, *Chaitophorus stevensis,* showed reduced predator-escape behavior in enriched CO_2 atmosphere, but greater escape behavior in enriched O_3 atmosphere, compared to ambient atmospheric conditions. Coûteaux *et al.* (1991) found that elevated CO_2 affected litter quality and decomposer food-web interactions. Ozone, but not nitrogen dioxide or sulfur dioxide, interfered with searching behavior and host discovery by a braconid parasitoid, *Asobara tabida.*

Disturbances affect species interactions in several ways. First, disturbances act like predators for intolerant species and reduce their population sizes, thereby affecting their interactions with other species. Second, disturbances contribute to landscape heterogeneity, thereby providing potential refuges from negative interactions (e.g., Denslow 1985). For example, disturbances often reduce abundances of predators, perhaps facilitating population growth of prey populations in disturbed patches (Kruess and Tscharntke 1994, Schowalter and Ganio 1999).

B. Resource Availability and Distribution

Resource availability affects competition and predation. If suitable resources (plants or animal prey) become more abundant, resource discovery becomes easier and populations of associated consumers grow. The probability of close contact and competition among consumers increases, up to a point at which the superior competitor(s) suppress or exclude inferior competitors. As a result, the intensity of interspecific competition may peak at intermediate levels of resource availability, although the rate of resource use may continue to rise with increasing resource availability (depending on functional and numeric responses). Population outbreaks reduce resource availability and also reduce populations of competing species.

Interactions are affected by the heterogeneity of the landscape. Potential competitors, or predators and their prey, often may not occur simultaneously in the same patches, depending on their respective dispersal and foraging strategies. Sparse resources in heterogeneous habitats tend to maintain small, low-density populations of associated species. The energetic and nutrient costs of detoxifying current resources or searching for more suitable resources limits growth, survival, and reproduction (see Chapters 3 and 4). Under these conditions, potentially interacting species are decoupled in time and space, co-occurring infrequently on a particular resource. Hence, competition is minimized and predator-free space is maximized in patchy environments. In contrast, more homogeneous environments facilitate population spread of associated species and maximize the probability of co-occurrence.

Palmer (2003) explored the effect of termite-generated heterogeneity in resource availability on the competitive interactions of four ant species that reside on acacia, *Acacia drepanolobium,* in East Africa. Only one ant species occupied an individual tree at any given time, and violent interspecific competition for host trees by adjacent colonies was common. Acacia shoot production and densities of litter invertebrates increased with proximity to termite mounds. The competitively dominant ant, *Crematogaster sjostedti,* displaced other acacia ants, *C. mimosae, C. nigriceps,* and *Tetraponera penzigi,* near termite mounds, whereas the probability of subordinate species displacing *C. sjostedti* increased with distance from termite mounds. This variation in the outcome of competition for acacia hosts appeared to result from differential responses among the ant species to resource heterogeneity on the landscape.

Species interactions also can affect habitat heterogeneity or resource availability. Cardinale *et al.* (2002) manipulated composition of three suspension-feeding caddisfly species at the same total density in experimental stream mesocosms. They reported that the total consumption of suspended particulate food was 66% higher in mixtures compared to single-species treatments. Facilitation of food capture by these potentially competing species in mixture resulted from increased stream bed complexity (reflecting variation in silk catchnet size), which in turn increased eddy turbulence and near-bed velocity, factors controlling the rate of food delivery.

C. Indirect Effects of Other Species

Ecologists traditionally have focused on pairs of species that interact directly (i.e., through energy or material transfers, as described earlier in this chapter). However, indirect interactions, such as reduced predation on mimics when the models are present, have received less attention but may be at least as important as direct effects. For example, pollinators can augment plant reproduction sufficiently to compensate for herbivory, thereby indirectly affecting plant–herbivore interaction (L. Adler *et al.* 2001, Strauss and Murch 2004). Batzer *et al.* (2000b) reported that indirect effects of predaceous fish on invertebrate predators and competitors of midge prey had a greater effect on midge abundance than did direct predation on midges.

Tritrophic-level interaction has been recognized as a key to understanding both herbivore–plant and predator–prey interactions (e.g., Boethel and Eikenbary 1986, Price *et al.* 1980). Even tritrophic-level interaction represents a highly simplified model of communities (Gutierrez 1986) in which species interactions with many other species are affected by changing environmental conditions (see Chapters 9 and 10). The tendency for multiple interactions to stabilize or destabilize species populations and community structure has been debated (Goh 1979, May 1973, 1983, Price 1997). May (1973) proposed that community stability depends on predator–prey interactions being more common than mutualistic interactions. Because multispecies interactions control rates of energy and nutrient fluxes through ecosystems, resolution of the extent to which indirect interactions contribute to stability of community structure will contribute significantly to our understanding of ecosystem stability.

Associated species affect particular interactions in a variety of ways. For example, much research has addressed the negative effects of plant defenses induced by early-season herbivores on later colonists (Fig. 8.11) (e.g., Harrison and Karban 1986, M. Hunter 1987, Kogan and Paxton 1983, N. Moran and Whitham 1990, Sticher *et al.* 1997, Van Zandt and Agrawal 2004, Wold and

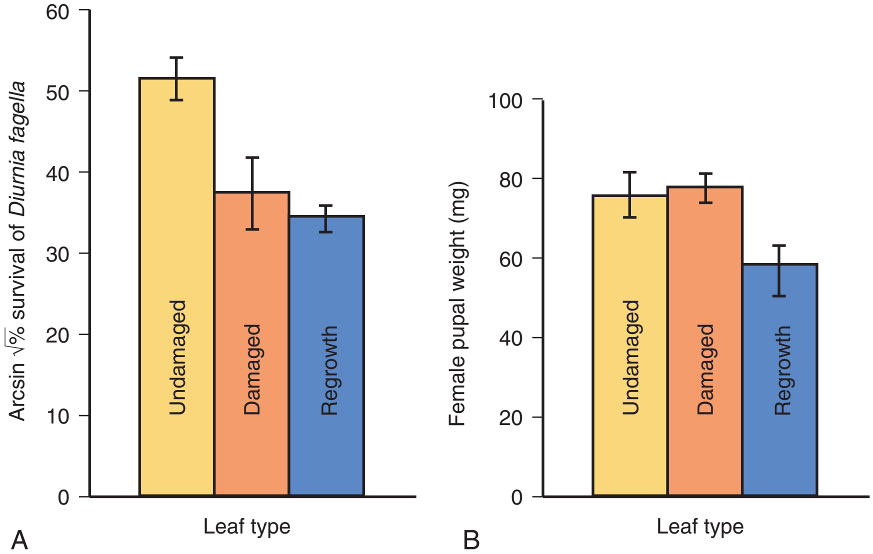


FIG. 8.11 Differential survival to pupation (*a*) and mean female pupal weight (*b*) of *Diurnea flagella* on foliage that was undamaged, naturally damaged by folivores, and produced following damage. Vertical lines represent standard errors of the mean. *Diurnea flagella* larvae feeding on regrowth foliage show both reduced survival to pupation and reduced pupal weight. From M. Hunter (1987) with permission from Blackwell Scientific.

Marquis 1997) and on decomposers (Grime *et al.* 1996). Survival and development of late-season herbivores usually are reduced by defenses induced by early-season herbivores.

Herbivore-induced defenses can affect other interactions as well. Callaway *et al.* (1999) reported that the tortricid moth, *Agapeta zoegana,* introduced to the western United States for biological control of spotted knapweed, *Centaurea maculosa,* increased the negative effect of its host on native grass, *Festuca idahoensis.* Reproductive output of grass was lower when neighboring knapweed had been defoliated by the moth, compared to grass surrounded by nondefoliated neighbors. Callaway *et al.* (1999) suggested that defenses induced by the moth also had allelopathic effects on neighboring plants or altered root exudates that affected competition via soil microbes.

Baldwin and Schultz (1983) and Rhoades (1983) independently found evidence that damage by herbivores can be communicated chemically among plants, leading to induced defenses in plants in advance of herbivory (see also Zeringue 1987). Although their hypothesis that plants communicate herbivore threat chemically with each other was challenged widely because of its apparent incongruency with natural selection theory (e.g., Fowler and Lawton 1985), studies have confirmed the induction of chemical defenses by volatile chemical elicitors, particularly jasmonic acid (Fig. 8.12) and ethylene (Farmer and Ryan 1990, McCloud and Baldwin 1997, Schmelz *et al.* 2002, Sticher *et al.* 1997, Thaler 1999a, Thaler *et al.* 2001). Jasomonate has been shown to induce production of proteinase inhibitors and other defenses against multiple insects and pathogens when applied at low concentrations to a variety of plant species (Fig. 8.13), including conifers (Hudgins *et al.* 2003, 2004, Thaler *et al.* 2001). Interplant communication via jasmonate has been demonstrated among unrelated species and even unrelated families (e.g., Farmer and Ryan 1990), although the fitness consequences of interspecific communication are not clear (Karban and Maron 2002). Thaler (1999b) demonstrated that tomato, *Lycopersicon esculentum,* defenses induced by jasmonate treatment doubled the rate of parasitism of armyworm, *Spodoptera exigua,* by the wasp, *Hyposoter exiguae.*

Endophytic or mycorrhizal fungi (see Chapter 3) can affect interactions between other organisms (E. Allen and Allen 1990, G. Carroll 1988, Clay 1990). G. Carroll (1988) and Clay *et al.* (1985) reported that mycotoxins produced by mutualistic endophytic fungi complement host defenses in deterring insect herbivores. Clay *et al.* (1993) documented complex effects of insect herbivores and

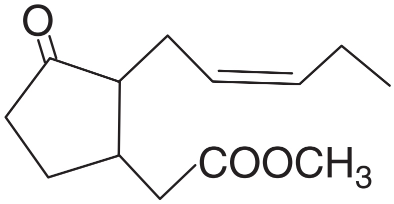


FIG. 8.12 Structure of methyl jasmonate, a volatile plant chemical that communicates plant damage and induces defensive chemical production in neighboring plants. From Farmer and Ryan (1990) with permission from National Academy of Sciences.

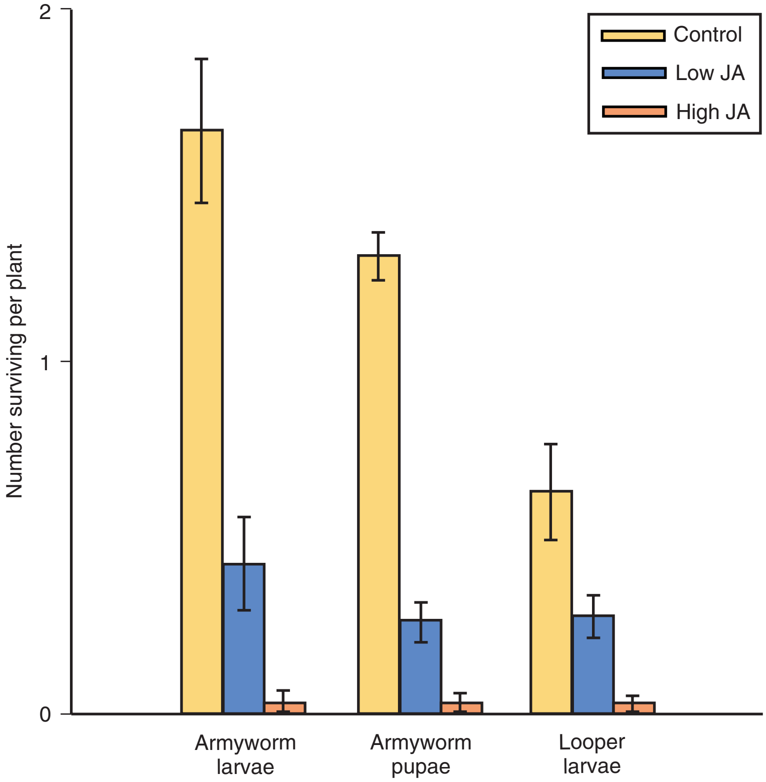


FIG. 8.13 Survival of beet armyworm, *Spodoptera oexigua*, larvae and pupae and cabbage looper, *Trichoplusia ni,* larvae on field-grown tomatoes sprayed with low (0.5 mM) or high (1.5 mM) doses of jasmonic acid, or unsprayed (control). Vertical lines represent 1 SE. From Thaler *et al.* (2001) with permission from Blackwell Scientific Ltd. Please see extended permission list pg 571.

endophytic fungi on the competitive interactions among grass species. For example, tall fescue, *Festuca arundinacea,* competed poorly with orchard grass, *Dactylis glomerata,* when herbivores were absent, but fescue infected with its fungal endophyte, *Acremonium* spp., competed better than either orchard grass or uninfected fescue when herbivores were present. Mycorrhizae transport nutrients among plants through the hyphal network, mediating plant competition (E. Allen and Allen 1990). Gange *et al.* (1999) and Goverde *et al.* (2000) experimentally inoculated plants with arbuscular mycorrhizal fungi and evaluated effects on aphids, *Myzus persicae,* and butterfly, *Polyommatus icarus,* larvae, respectively. In both studies, mycorrhizal inoculation increased insect growth and survival, apparently related to increased P concentrations in foliage of mycorrhizal plants. Goverde *et al.* (2000) further reported that herbivore performance was related to the species of mycorrhizae colonizing the host plant. Sooty molds growing on foliage may affect palatability for herbivores (Fig. 8.14).

Volatile defenses of plants induced by defoliators often attract the herbivore's predators and parasites (e.g., Kessler and Baldwin 2001, Price 1986, Thaler *et al.* 1999b, Turlings *et al.* 1990, 1993, 1995). At the same time, however, plant defenses sequestered by herbivores can affect herbivore–predator and herbi-

FIG. 8.14 Indirect effects of associated species. The light-colored foliage at the ends of shoots is new grand fir, *Abies grandis,* foliage produced during 1994, a dry year, in western Washington; the blackened 1993 foliage was colonized by sooty mold during a wet year; normal foliage prior to 1993 was produced during extended drought. Sooty mold exploits moist conditions, especially honeydew accumulations and, in turn, may affect foliage quality for folivores.

vore–pathogen interactions (L. Brower *et al.* 1968, Stamp *et al.* 1997, Tallamy *et al.* 1998, Traugott and Stamp 1996). Inflorescence spiders preying on pollinators affect the pollinator–plant interaction (Louda 1982). Herbivores feeding above ground frequently deplete root resources through compensatory translocation and negatively affect root-feeding herbivores (e.g., Masters *et al.* 1993, Rodgers *et al.* 1995, Salt *et al.* 1996).

Chilcutt and Tabashnik (1997) examined the effect of diamondback moth, *Plutella xylostella,* resistance to *Bacillus thuringiensis* on within-host interactions between the pathogen and the parasitoid wasp, *Cotesia plutellae.* Resistant caterpillars reduced the success of both pathogen and parasitoid. In susceptible caterpillars, by contrast, the pathogen had a significant, negative effect on the parasitoid, but the parasitoid had no effect on the pathogen. In moderately resistant hosts, competition between the pathogen and parasitoid was symmetrical:

each had a significant negative effect on the other. Highly resistant hosts provided a refuge from competition for the parasitoid.

Ants affect, and are affected by, a variety of other interactions. Ants attracted to domatia, to floral or extrafloral nectories, or to aphid honeydew commonly affect herbivore–plant interactions (Cushman and Addicott 1991, Fritz 1983, Jolivet 1996, Oliveira and Brandâo 1991, Tilman 1978). The strength of this interaction varies inversely with distance from ant nests. Tilman (1978) reported that ant visits to extrafloral nectaries declined with the distance between cherry trees and ant nests. The associated predation on tent caterpillars by nectar-foraging ants also declined with distance from the ant nest.

Currie (2001) and Currie *et al.* (1999a, b) reported complex interactions between fungus-growing ants, especially leaf-cutting species of *Atta* and *Acromyrmex,* their mutualistic fungi, species of *Leucocoprinus* and *Leucoagaricus,* and associated microorganisms. The ants provide live or dead vegetable material for fungal decomposition, tend the gardens by weeding alien microbes, and feed on the fungus. Foundress queens carry fungus inoculum to establish new colonies. The fungus gardens have been discovered to host a virulent fungal pathogen, *Escovopsis,* capable of destroying the fungus garden and the dependent ant colony. The ants have an additional mutualistic association with an actinomycete bacterium that produces specialized antibiotics with potent inhibitory activity against *Escovopsis.*

Similarly complex interactions among a community of invertebrates and fungi affect bark beetle interactions with host trees (see earlier in this chapter). The southern pine beetle once was thought to have a mutualistic association with blue-stain fungi, with beetles providing transport and the fungus contributing to tree death and beetle reproduction. However, several studies have shown that this beetle can colonize trees in the absence of the fungus (Bridges *et al.* 1985); that the blue-stain fungus is, in fact, detrimental to beetle development and is avoided by the mining beetles (Barras 1970, Bridges 1983, Bridges and Perry 1985); and that other mycangial fungi are necessary for optimal beetle development (Ayres *et al.* 2000, Bridges and Perry 1985). Subsequent research demonstrated that phoretic tarsonemid mites collect spores of the blue-stain fungus in specialized structures, *sporothecae* (Fig. 8.15) (Bridges and Moser 1983, Moser 1985). Beetles carrying these mites transport the blue-stain fungus significantly more often than do mite-free beetles (Bridges and Moser 1986). The beetle–tree interaction is affected further by phoretic predaceous mites that prey on nematode parasites of the beetle (Kinn 1980). Finally, folivorous insects increase tree susceptibility to colonization by bark beetles (Wallin and Raffa 2001).

Termite interaction with mutualistic gut symbionts is affected by host wood and associated fungi. Using forced feeding and preference tests involving combinations of several conifer species and fungi, Mankowski *et al.* (1998) found that termite preferences for wood–fungal combinations generally reflected the suitability of the resource for the gut fauna, as indicated by changes in gut faunal densities when termites were forced to feed on wood–fungus combinations.

Competitive interactions between a pair of species may be modified by the presence of additional competitors. Pianka (1981) proposed a model in which two species with modest competitive overlap over a range of resource values could

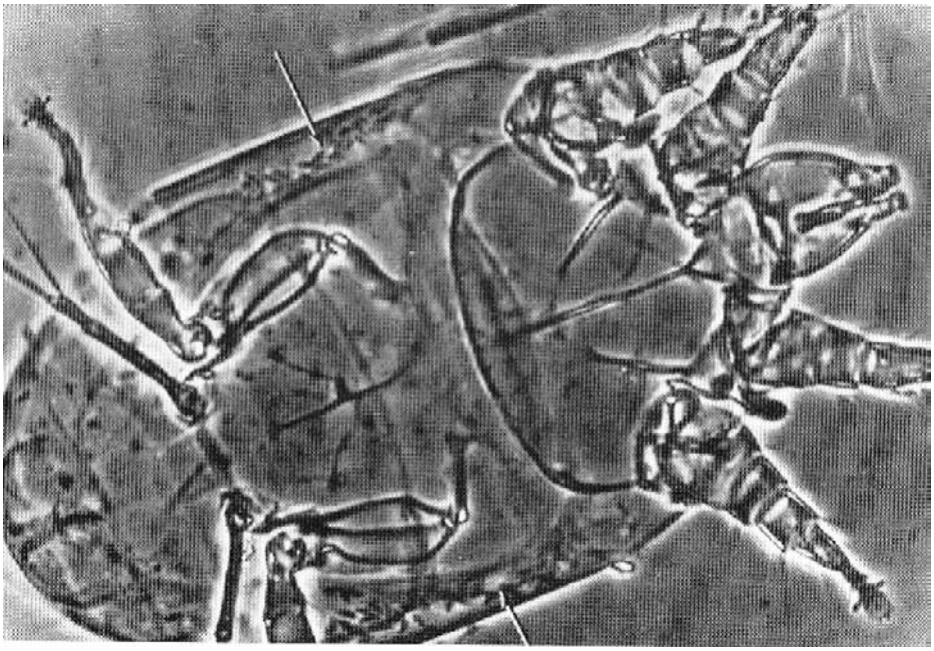


FIG. 8.15 Ascospores of *Ceratocystis minor* in sporothecae (*arrows*) formed by tergite 1 on the ventral-lateral sides of a *Tarsonemus ips* female, phoretic on the southern pine beetle, *Dendroctonus frontalis*. From Moser (1985) with permission from the British Mycological Society.

become "competitive mutualists" with respect to a third species that could compete more strongly for intermediate resource values. The two species benefit each other by excluding the third species from both sides of its resource spectrum (niche).

Competitive interactions among several species also can be modified by predators. A predator that preys indiscriminately on several competing prey species, as these are encountered, will tend to prey most often on the most abundant prey species, thereby preventing that species from competitively suppressing others. R. Paine (1966, 1969a, b) introduced the term *keystone species* to refer to top predators that maintain balanced populations of competing prey species. However, this term has become used more broadly to include any species whose effect on community and ecosystem structure or function is disproportionately large, compared to its abundance (Bond 1993, Power *et al.* 1996). Some insect species play keystone roles. For example, many herbivorous insects affect plant competitive interactions by selectively reducing the density of abundant host species and providing additional space and resources for nonhost plants (Louda *et al.* 1990a, Schowalter and Lowman 1999), thereby affecting resources available for associated species.

Although it often is convenient to emphasize the adaptive aspects of species interactions, especially symbiotic interactions, modern associations may not represent co-evolved relationships. Connell (1980) noted that niche partitioning and other adaptations that minimize competition among living species may reflect competition among their ancestors. Janzen and Martin (1982) suggested that current seed-dispersing animals may have replaced extinct species with which plants co-evolved mutualistic associations in the past. For example, large-seeded fruits in North and South America may reflect adaptation for dispersal by extinct gomphotheres and ground sloths; smaller extant vertebrates now perform this role but are much less capable of transporting such seeds over distances necessary for colonization.

III. CONSEQUENCES OF INTERACTIONS

A given species interacts with many other species in a variety of ways (competing for various food, habitat, and other resources; preying or being preyed on; and cooperating with mutualists) with varying degrees of positive and negative feedback on abundance. Therefore, the population status of species in the community represents the net effects of these positive and negative feedbacks.

A. Population Regulation

As discussed in Chapter 6, competition and predation have been recognized as two primary mechanisms, along with resource quality and quantity, for limiting population growth of a given species (e.g., May 1983). Any particular species usually interacts with at least 2–5 other species as prey (see Chapter 9) and with additional species as a competitor. Life table analysis often is used to identify key factors, especially predators or other interactions, that contribute most to population change, but the combination of interactions provides for "redundant" control of population growth. If the major regulating species should disappear, other predators, parasites, or competitors usually compensate.

As noted earlier in the chapter, mutualistic interactions may reduce the probability that either species will decline to extinction. Mutualistic species often are closely associated, especially in obligate relationships, and enhance each other's resource acquisition, energy and nutrient balance, or reproduction. Although mutualism is likely to become unstable at low population densities of either partner, depending on the degree of obligation (May 1983), mutualism could help to maintain the two populations above extinction thresholds (Dean 1983).

The combination of various interactions involving a particular species should maintain its population levels within a narrower range than would occur in the absence of these various interactions. Croft and Slone (1997) found that three predaceous mite species maintained populations of the European red mite, *Panonychus ulmi,* at lower equilibrium levels than did fewer predator species. However, few studies have documented the importance of species diversity or food web structure to the stability of population levels.

B. Community Regulation

The extent to which the network of regulatory interactions maintains stable community structure (see Chapters 9, 10, and 15) has been a topic of considerable debate. Although some irruptive species show wide amplitude in population size over time and space, such irruptions often reflect disruption of normal interactions as a result of anthropogenic habitat alteration or introduction into new habitats (see Chapters 6 and 7). The range in population size may be narrower, and the duration of deviations shorter, when regulatory interactions are intact.

The capacity for the network of interactions to stabilize species populations may be enhanced by compensatory interactions and changes in the nature or strength of interaction with changing environmental conditions. For example, the many plant species at a site can, at the same time, compete for resources, share nutrients via mycorrhizae, be growth-limited by herbivores, and limit herbivore populations through the mingling of attractive host odors and repellent (or unattractive) nonhost odors (E. Allen and Allen 1990, A. Hunter and Arssen 1988, Visser 1986). The net result of these negative and positive effects of interaction may be balanced co-existence (W. Carson and Root 2000). Ants maximize energy gain by preying on aphids when the value of honeydew rewards is low (e.g., scattered individuals or individuals dispersing from dense colonies) and by tending aphids when the value of honeydew rewards is high (Bristow 1991, Cushman and Addicott 1991). Competitive interactions could become mutualistic if two competitors mutually exclude a third, more competitive, species from the intermediate region of the shared niche (Pianka 1981). Such flexibility in species interactions may facilitate regulation in a variable environment. If the various species in the community respond to changes in each other's population densities in ways that are neutral or beneficial at low densities and increasingly negative at higher densities (see Chapters 12 and 15), then community structure should be relatively stable. Stabilization of community structure has substantial implications for the stability of ecosystem processes (see Chapter 15).

Interactions strongly affect energy or nutrient balances, survival, and reproduction of the associated species and therefore represent major selective factors. Strongly negative interactions should select for adaptive responses that minimize the negative effect (e.g., niche partitioning among competitors, prey defenses, etc.). Therefore, negative interactions should evolve toward more neutral or mutualistic interactions (G. Carroll 1988, Price 1997).

IV. SUMMARY

Species interact in a variety of ways with the other species that co-occur at a site. These interactions produce combinations of positive, neutral, or negative effects for species pairs. However, other species may alter the nature or strength of particular pairwise interactions (e.g., predators can reduce the intensity of competition among prey species by maintaining their populations below levels that induce competition).

Some species compete for a shared resource, with the result that the per capita share of the resource is reduced. This interaction has negative effects on both species. Competition can be by exploitation, when all individuals have equal access to the resource, or interference, when individuals of one species preempt use of, or defend, the resource. In cases of asymmetrical competition, the superior competitor can exclude inferior competitors over a period of time (competitive exclusion), unless the inferior competitor can escape through dispersal or survival in refuges where superior competitors are absent.

Predator–prey interactions involve a predator killing and eating prey and therefore have a positive effect on the predator but a negative effect on the prey. Predators and parasites affect prey populations similarly, but predators generally are opportunistic with respect to prey taxa and kill multiple prey per individual, whereas parasites generally are more specialized for association with particular host species and may or may not kill the host. Predators show preferences for prey size or defensive capability that maximize capture and utilization efficiency.

Symbiosis involves an intimate association between a symbiont and its host species, often co-evolved to maximize the probability of association and to mitigate any host defense against the symbiont. Symbiosis includes parasitism, commensalism, and mutualism. Parasitism is beneficial to the parasite but detrimental to its host. Although parasitism usually is considered to involve animal hosts, insect herbivores have a largely parasitic association with their host plants. Parasitoidism is unique to insects and involves an adult female ovipositing on or in a living host, with her offspring feeding on and eventually killing the host. Most hosts of parasitoids are other arthropods, but at least one sarcophagid fly is a parasitoid of tropical lizards. Commensalism benefits the symbiont but has neutral effects for the host. Usually the symbiont uses the host or its products as habitat or as a means of transport with negligible effects on the host. Mutualism benefits both partners and is exemplified by pollinator–plant, ant–plant, ant–aphid, and detritivore–fungus interactions.

A variety of factors influence the nature and intensity of interaction. Abiotic factors that affect the activity or condition of individuals of a species may alter their competitive, predatory, or defensive ability. Resource availability, particularly the quality and patchiness of resources, may mitigate or exacerbate competition or predation by limiting the likelihood that competitors, or predators and their prey, co-occur in time and space. Other species can influence pairwise interactions indirectly. For example, predators often reduce populations of various prey species below sizes that would induce competition. Induced plant responses can influence predator–herbivore interactions and competition among herbivores in time and space. Species whose presence significantly affects diversity or community structure have been considered keystone species. A number of insect species function as keystone species.

Competition and predation/parasitism have been recognized as important mechanisms of population regulation and have been amenable to mathematical modeling. Mutualism has been viewed largely as a curiosity, rather than an important regulatory interaction, and modeling efforts have been more limited. However, mutualism may promote both populations and reduce their risk of decline to unstable levels. The network of interactions affecting a particular species may maintain population size within a narrower range with less frequent irruptions than occurs when populations are released from their regulatory network. The extent of mutual regulation (stabilization) of populations through this network of interactions has been widely debated but has significant implications for the stability of community structure and ecosystem processes governed by these interactions.

9

Community Structure

A COMMUNITY IS COMPOSED OF ALL THE ORGANISMS OCCUPYING A SITE. The extent to which these organisms are co-evolved to form a consistent and recurring integrated community or represent *ad hoc* assemblages of loosely interacting species remains a topic of much discussion. Considerable research has been directed toward identifying spatial and temporal patterns in community structure and evaluating factors that determine community composition. Such efforts have become increasingly important to conservation efforts, with recognition that many species depend on the presence of associated species. However, comparison of community structures within, or among, broadly distributed community types that share few, if any, species requires approaches that are independent of the taxonomic composition of the community.

Ecologists have developed a variety of nontaxonomic approaches to describing community structure, providing different types of information to meet different objectives. The diversity of approaches has hindered comparison of communities described in different terms. Nevertheless, distinct geographic patterns can be seen in community structure, and some community types characterize particular habitat conditions. A number of factors determine community composition, distribution, and dynamics. This chapter focuses on approaches to describing community structure and on biogeographic patterns and underlying factors contributing to community structure. Temporal patterns in community structure are the focus of the next chapter.

I. APPROACHES TO DESCRIBING COMMUNITIES

Although the community is understood to include all organisms at a site, for practical reasons most studies have addressed subsets of this community. Hence, the literature on communities includes references to the plant community, the arthropod community, the bird community, consumer communities associated with different plant species, tritrophic interactions, etc. Insects have been addressed to varying degrees in studies of communities, although insects represent the majority of species in terrestrial and freshwater aquatic communities (Table 9.1) and clearly are integral to community structure and dynamics (e.g., as pollinators or herbivores of vegetation, as resources for vertebrates, etc.). Description of particular subsets of the community involves further differentiation in approaches.

Three general approaches to describing community structure can be identified: species diversity, species interactions, and functional organization. Although the “ideal” approach is a topic of intense ecological debate (e.g., Polis 1991a), each approach provides useful information, and the choice largely reflects objectives and practical considerations. Where possible, combining approaches can yield a broader description of the community.

A. Species Diversity

Insects represent the vast majority of species in terrestrial and aquatic ecosystems. For example, in most ecosystems where diversity of insect or arthropod species has been inventoried, along with plants and vertebrates, arthropods account for 70–90% of the total number of recorded species (see Table 9.1), roughly the same proportion as the total number of described species of organisms. Given that plant and vertebrate inventories are relatively complete, whereas currently described insect species represent only a fraction of the estimated total number of species (May 1988, Sharkey 2001, E. Wilson 1992), the proportional representation of invertebrates likely will increase.

Species diversity is a central theme in ecology. An enormous amount of research has addressed how diversity develops under different environmental conditions, how anthropogenic changes are affecting diversity, and how diversity affects the stability of natural communities (see Chapters 10 and 15). Clearly, the measurement of diversity is fundamental to meeting these objectives.

Diversity can be represented in various ways (Magurran 2004). The simplest representation is a catalog of species, or the total number of species (richness), a measure that indicates the variety of species in a community (α diversity). Rarely can all species be detected and documented. Usually the number of species recorded increases with the number of samples collected. The total number of species can be estimated by extrapolating from a species abundance curve that plots cumulative species against cumulative sample number or area. Alternatively, several parametric and nonparametric estimators can be used (Magurran 2004). Species richness can be standardized for various ecosystems by measuring the number of species per unit area or per 1000 individuals.

TABLE 9.1 Numbers of species of vascular plants, vertebrates, and arthropods in desert, grassland, forest, and aquatic ecosystems.

Ecosystem	Vascular Plants	Vertebrates	Arthropods	% Arthropods
Desert				
USSR[a]	125	98	>1360	75
Southwestern United States 1[a]	174	145	>1100	77
Southwestern United States 2[a]	>600	201	>2640	77
Grassland/Savanna				
Hungary[b]	1311	347	8496	93
Hungary[c]	1762	289	7095	78
Central United States[d]	521	355	>1750	67
Forest				
Conifer, western United States[e]	600	88	>3500	84
Deciduous, eastern United States[f]	2816	450	>4300	57
Tropical, Puerto Rico[g]	470	78	>1500	73
Marsh				
Hungary[h]	804	118	5332	85
Stream				
Tropical, Puerto Rico[i]	0	7	50	88
Lake				
Balaton, Hungary[j]	>9	51	>1200	95

[a] Data from Polis (1991b).
[b] Data from Mahunka (1986, 1987) and Szujko–Lacza and Kovacs (1993).
[c] Data from Mahunka (1981, 1983) and Szujko–Lacza (1982).
[d] Data from Hazlett (1998) and Lavigne *et al.* (1991); arthropod data are for insects only.
[e] Data from G. Parsons *et al.* (1991).
[f] Data from Sharkey (2001).
[g] Data from Garrison and Willig (1996), W. Lawrence (1996), and Reagan *et al.* (1996).
[h] Data from Mahunka (1991).
[i] Data from Covich and McDowell (1996); no vascular plants represented in this headwater stream.
[j] Data from Benedek (1988).

This measure of diversity accounts for the typical increase in number of species with increasing sample area or number of individuals.

Species richness for many plant and animal groups increases from high latitudes to lower latitudes and from smaller, more isolated islands to larger islands near continents (MacArthur and Wilson 1967, Magurran 2004, Stiling 1996). Richness also increases from harsh or frequently disturbed ecosystems that restrict richness to more productive ecosystems that provide a greater number of niches but usually declines again in very productive ecosystems (Tilman and Pacala 1993). Species diversity appears generally to peak at intermediate levels of disturbance (the *intermediate disturbance hypothesis*) as the result of a combination of sufficient resources and insufficient time for competitive exclusion (Connell 1978, Huston 1979, Lubchenco 1978, Pickett and White 1985, Sousa 1979). Insect diversity may reflect primarily the diversity of plants, which affects diversity of host resources and habitat structure (Curry 1994, Magurran 2004, Stiling 1996).

The various species in a community are not equally abundant. Usually a few species are abundant and many species are represented by only one or a few individuals. The distribution of numbers of individuals among species (evenness) is a measure of each species' importance. Rank-abundance curves are a commonly used method of presenting species abundance data (Magurran 2004). Four rank-abundance patterns are most commonly used for comparison among different communities (Fig. 9.1). The *geometric model* (or *niche-preemption hypothesis*) describes a community in which successively less abundant species use the same proportion of resources available after preemption by the more abundant species. This situation is predicted to occur when species arrive in an unsaturated community at regular time intervals and exploit a fraction of the remaining resources. The *log series model* is closely related to the geometric model but is predicted to occur when the time intervals between species arrival are random rather than regular. The *log normal model* has been shown to be widely applicable because this distribution results mathematically from random variation

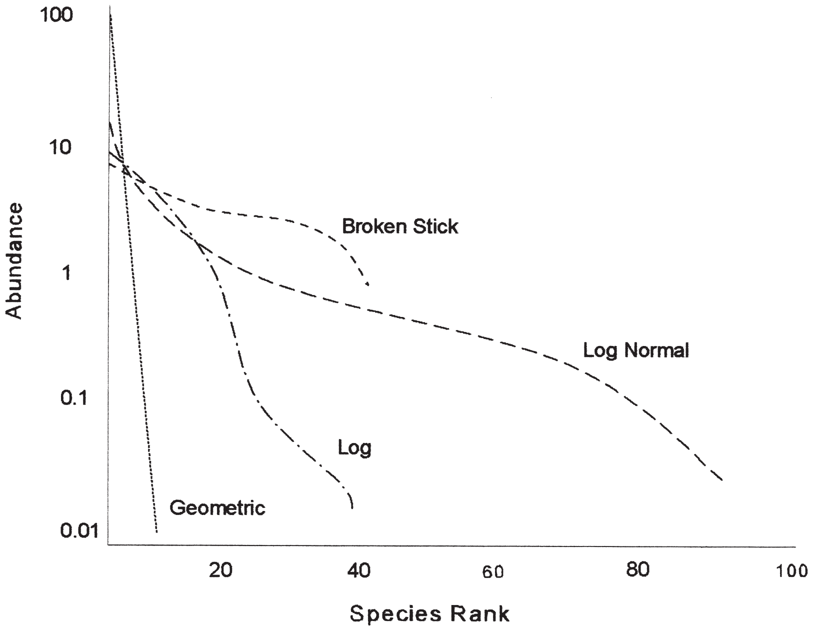


FIG. 9.1 Typical shapes of four rank-abundance models. Species are ranked from most to least abundant. Redrawn from Magurran (1988).

among a large number of factors producing a normal distribution. In natural communities, the large number of environmental factors affecting species abundances fulfills this condition. This condition also can be met by increasing numbers of species randomly partitioning available niches. The *broken stick model* reflects relatively uniform use of resources among species in the community. Generally, as richness and evenness increase, the rank-abundance pattern shifts from a geometric pattern to a log pattern and finally to a broken stick pattern. Disturbances and other environmental changes can alter rank-abundance patterns (Figs. 9.2 and 9.3) (Bazzaz 1975, Kempton 1979).

Richness and evenness have been combined mathematically in various ways to calculate diversity indices based on proportional abundances of species (e.g., Magurran 2004, Stiling 1996). Two indices have been used widely, the Shannon-Wiener, or Shannon (often incorrectly referred to as the Shannon-Weaver) index, and Simpson's index. The two indices differ in their emphasis on species richness (Shannon-Wiener) or abundance (Simpson's).

The Shannon-Wiener index assumes that individuals are randomly sampled from an effectively infinite population and that all species are represented in the sample. Diversity (H') is calculated as follows:

$$H' = -\sum_{i=1}^{n} p_i \ln p_i \tag{9.1}$$

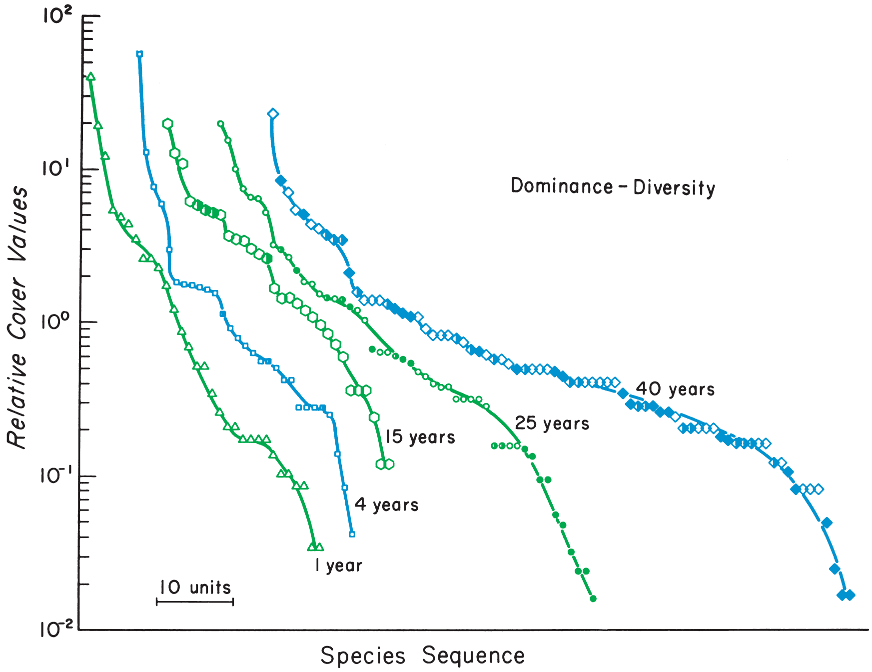


FIG. 9.2 Rank-abundance curves for old fields representing five postabandonment ages in southern Illinois. Open symbols are herbs, half-open symbols are shrubs, and closed symbols are trees. From Bazzaz (1975) with permission of the Ecological Society of America.

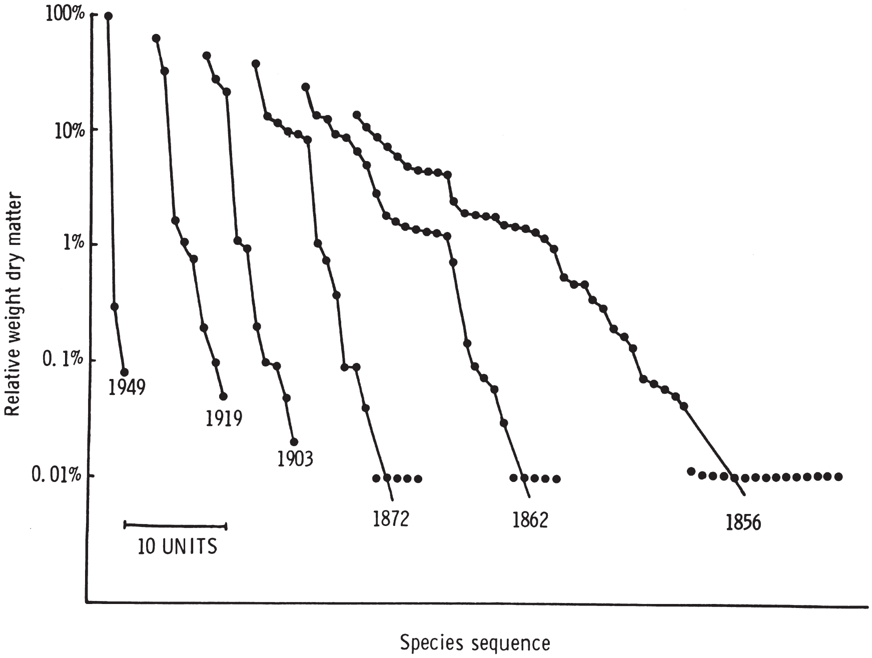


FIG. 9.3 Change over time in rank abundance of plant species in an experimental plot of permanent pasture at Rothamsted, United Kingdom, following continuous application of nitrogen fertilizer since 1856. Species with abundances < 0.01% were recorded as 0.01%. From Kempton (1979) with permission from the International Biometric Society.

where p_i is the proportion of individuals found in the *i*th species. Values generally fall in the range 1.5–3.5, rarely surpassing 4.5. If the rank-abundance pattern follows a log normal model, 10^5 species are necessary to produce a value of $H' > 5$. If the index is calculated for a number of samples, the indices will be normally distributed and amenable to use of parametric statistics, including ANOVA (analysis of variance), to compare diversities among sets of samples (Magurran 2004) (e.g., to evaluate the effects of ecosystem change; Fukami *et al.* 2001). If all species were equally abundant, a maximum diversity (H_{max}) can be calculated as ln S, where S is the total number of species. The ratio of observed to maximum diversity is a measure of evenness.

When randomness cannot be assured (e.g., data from light trapping, with species representation based on differential attraction to light), the Brillouin index is a more appropriate measure of diversity (Magurran 2004). This index (HB) is calculated as follows:

$$HB = (\ln N! - \sum \ln n_i!)/N \tag{9.2}$$

where N is the total number of individuals and n_i is the number of individuals in the *i*th species. Values of this index rarely exceed 4.5 and generally are correlated with, but lower than, Shannon indices for the same data.

Simpson's index differs from the Shannon-Wiener and Brillouin indices in being weighted toward the abundances of the most common species, rather than species richness (Magurran 2004). This index (D) is calculated as follows:

$$D = \sum_{i=1}^{n} (n_i(n_i - 1))/(N(N-1)) \tag{9.3}$$

where n_i is the number of individuals in the ith species and N is the total number of individuals. Diversity decreases as D increases, so Simpson's index generally is expressed as 1 – D or 1/D. Once the number of species exceeds 10, the underlying rank-abundance pattern is important in determining the value of D.

Diversity indices have been a tool for comparing taxonomically distinct communities based on their rank-abundance patterns. However, important information is lost when species diversities are reduced to an index (Magurran 2004). For example, a larger diversity index can reflect the influence of increased abundances of invasive or exotic species without conveying important information about the change in community integrity or function. Very different community structures can produce the same diversity index. Furthermore, ecologically unique communities are not necessarily diverse and would be lost if conservation decisions were made on the basis of diversity alone (Magurran 2004).

The large number of species represented by single individuals ("singletons") poses a dilemma (Novotný and Basset 2000). Should these be included in diversity calculations? Their presence may be accidental or reflect inadequate or biased sampling. Novotný and Basset (2000) found that singletons consistently represented 45% of herbivores sampled among plant species. Some singletons represented species that were more common on other plant species, whereas others represented species that were relatively rare on numerous host plants. Novotný and Basset (2000) concluded that singletons are an important component of communities and should not be excluded from community studies as an artifact or a group of negligible importance.

Diversity also can be measured as variation in species composition among communities or areas (β diversity). Several techniques have been developed to compare communities, based on their species compositions and rank-abundance patterns, across environmental gradients or between areas (Magurran 2004).

The simplest of these similarity measures are indices based on species presence or absence in the communities being compared. The Jaccard index (C_J) is calculated as follows:

$$C_J = j/(a + b - j) \tag{9.4}$$

and the Sorenson index (C_S) is calculated as follows:

$$C_S = 2j/(a + b) \tag{9.5}$$

where j is the number of species found in both sites, a is the number of species in the first site, and b is the number of species in the second site. Neither of these indices accounts for species abundances.

Three quantitative similarity indices have been used widely. A modified version of the Sorenson index (C_N) is calculated as follows:

$$C_N = 2\,jN/(aN + bN) \tag{9.6}$$

where jN is the sum of the lower of the two abundances for each species found in both sites, aN is the total number of individuals in the first site, and bN is the total number of individuals in the second site. Most quantitative similarity indices are influenced strongly by species richness and sample size. The Morisita-Horn index (C_{mH}) is influenced less by species richness and sample size but is sensitive to the abundance of the dominant species. Nevertheless, it may be generally a satisfactory similarity index (Magurran 2004). This index is calculated as follows:

$$C_{mH} = 2\sum(an_i bn_i)/(da + db)aN \times bN \tag{9.7}$$

where aN is the total number of individuals in the first site, an_i is the number of individuals of the *i*th species in the first site, and $da = \Sigma an_i^2/aN^2$. The Bray-Curtis Similarity Index also has been shown to be effective and robust (Minchin 1987). This index is calculated as follows:

$$C_B = \left(1 - \sum_{i=1}^{n} |X_{ij} - X_{ik}| \middle/ \sum_{i=1}^{n} (X_{ij} + X_{ik})\right) \tag{9.8}$$

where n is the number of species and X_{ij} and X_{ik} are the number of individuals of the *i*th species at sites j and k, respectively (Cartron *et al.* 2003).

More recently, multivariate statistical techniques have been applied to comparison of communities. Cluster analysis can be performed using either presence–absence or quantitative data. Each pair of sites is evaluated on the degree of similarity, then combined sequentially into clusters to form a dendrogram with the branching point representing the measure of similarity (Figs. 9.4 and 9.5). Ordination compares sites on their degree of similarity, then plots them in Euclidian space, with the distance between points representing their degree of similarity (Figs. 9.6 and 9.7). Ordination techniques include principal components analysis (PCA), detrended correspondence analyses (DCA), and nonmetric multidimensional scaling (NMS).

Minchin (1987) evaluated several commonly used ordination techniques for sensitivity to sampling pattern, data distribution, and geometric distortion. PCA and principle coordinates analysis both suffered from curvilinear distortion, and DCA lacked robustness to variation in sampling pattern and response model. NMS was shown to be the most robust ordination method and is becoming more widely used in ecological studies.

Both cluster and ordination techniques can indicate which species or environmental factors contribute most to the discrimination of groupings. Indicator species analysis (Dufrêne and Legendre 1997) is another method that can be used to identify species or groups of species that characterize groups of sites, based on ecological gradients or treatments, by combining the frequency of a species occurrence in a particular site category and its degree of restriction to that site category. Dufrêne and Legendre (1997) compared this method with

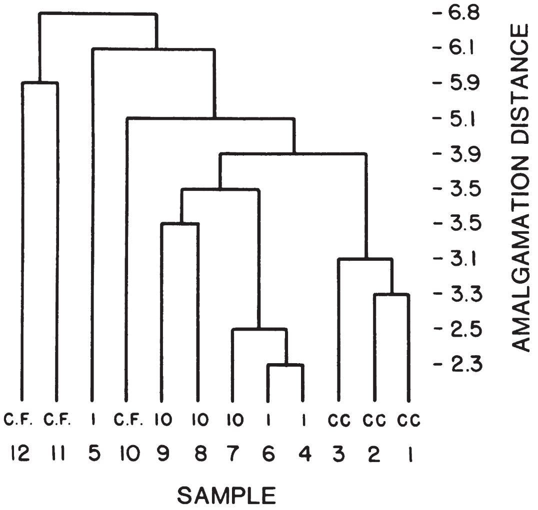


FIG. 9.4 Dendrogram of similarity for dung beetles in clearcuts, 1 ha and 10 ha forest fragments, and contiguous forest. From Klein (1989) with permission from the Ecological Society of America.

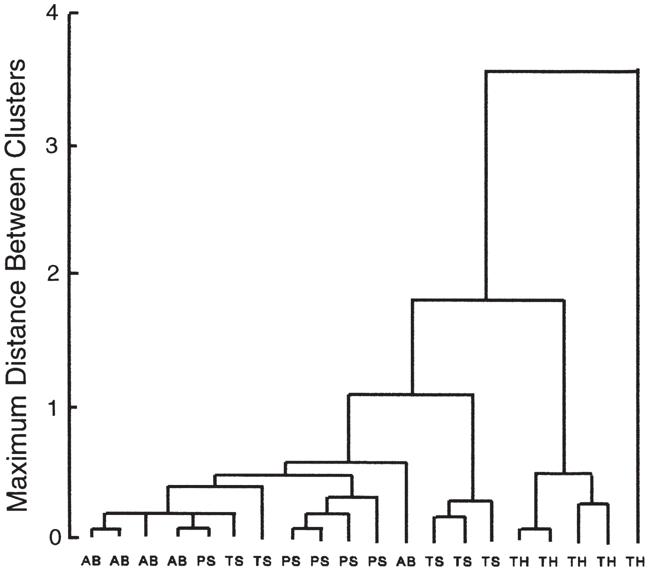


FIG. 9.5 Dendrogram of arthropod community similarity in canopies of four old-growth conifer species at the Wind River Canopy Crane Research Facility in southwestern Washington. AB, *Abies grandis* (grand fir); PS, *Pseudotsuga menziesii* (Douglas fir); TS, *Tsuga heterophylla* (western hemlock); and TH, *Thuja plicata* (western redcedar). Data from Schowalter and Ganio (1998).

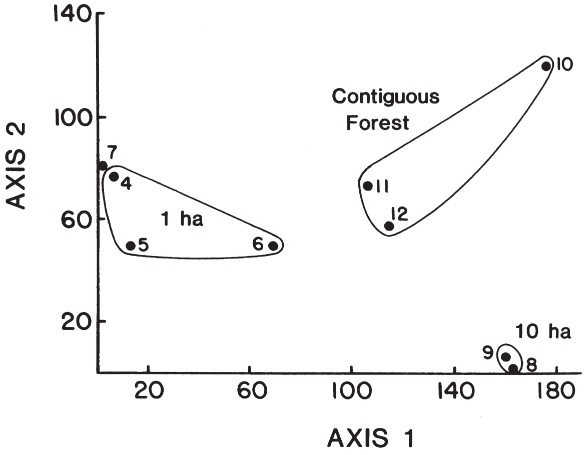


FIG. 9.6 Detrended correspondence analysis ordination of dung beetle assemblages in clearcuts, 1 ha and 10 ha forest fragments, and contiguous forest. From Klein (1989) with permission from the Ecological Society of America.

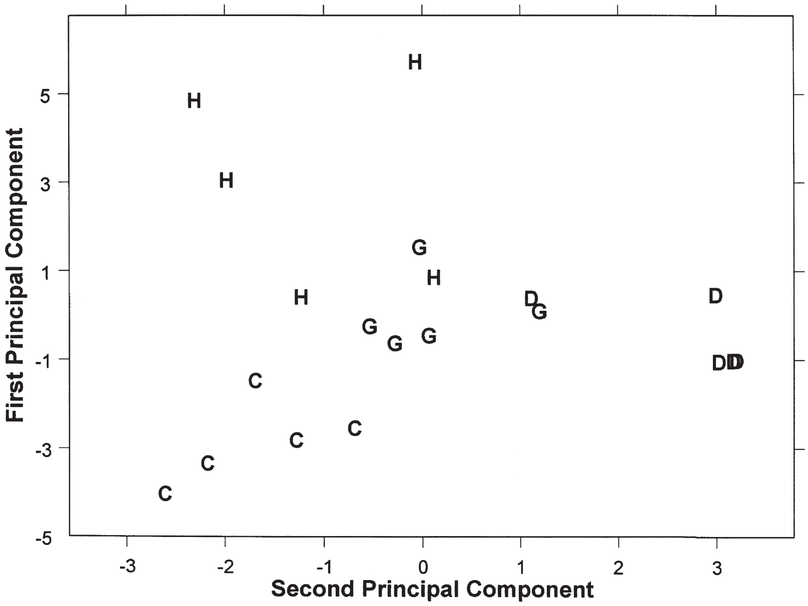


FIG. 9.7 Principle components analysis ordination of arthropod communities in canopies of four old-growth conifer species at the Wind River Canopy Crane Research Facility in southwestern Washington. G, grand fir *(Abies grandis)*; D, Douglas fir *(Pseudotsuga menziesii)*; H, western hemlock *(Tsuga heterophylla)*; and C, western red cedar *(Thuja plicata)*. From Schowalter and Ganio (1998) with permission from CAB International.

clustering and ordination techniques to identify carabid beetle species characterizing combinations of soil moisture and alkalinity represented by 69 sites in Belgium.

The significance of differences among groups of points representing sites, treatments, etc., can be analyzed using multiple response permutation procedures (MRPP) (Biondini *et al.* 1988). This method measures the separation among weighted means of points in *a priori* groups and tests the probability of occurrence of this mean relative to other possible separations with the same size structure that could have occurred for these points (Biondini *et al.* 1988).

B. Species Interactions

Communities can be characterized in terms of the relationships among species, most commonly trophic (feeding) interactions (i.e., food webs). Clearly, the most complete description of the community would include all possible interactions (including indirect interactions) among the total number of species (e.g., Polis 1991a). In practice, this is difficult to accomplish, even in relatively species-poor communities (Camilo and Willig 1995, Polis 1991a, 1991b, Reagan *et al.* 1996) because of the largely unmanageable number of arthropod species (Table 9.1) and lack of complete information on their interactions. More commonly, research focuses on subsets or simplified representations of the community.

The simplest approach to community description emphasizes interactions between only a few species (e.g., plant–herbivore or predator–prey interactions). In particular, many studies have addressed the relatively distinct assemblages of arthropods based on individual plant species (e.g., Richerson and Boldt 1995, Schowalter and Ganio 1998) or soil/litter resources (e.g., J. Moore and Hunt 1988, Seastedt *et al.* 1989). This approach maximizes description of interactions among a manageable number of relatively resource-specific herbivores or detritivores and their associated predators and parasites. Detailed descriptions at this level have been useful for identifying and comparing factors affecting these trophic interactions (e.g., chemical defenses; see Chapters 3 and 8), for evaluating the coevolutionary patterns of speciation between insects and their hosts (e.g., Becerra 1997), and for comparing trophic interactions among community types (e.g., comparing phenological responses of insect herbivores to leaf emergence in tropical and temperate forests; Coley and Aide 1991). However, this approach emphasizes relatively linear trophic relationships (i.e., food chains) and does not address linkages among members of different component communities.

Broader subcommunities can be identified. For example, Hunt *et al.* (1987) described the trophic interactions among arthropod and microbial species composing the litter subcommunity of a grassland ecosystem. J. Moore and Hunt (1988) subsequently noted that relatively discrete component communities supported by particular resource bases (bacteria, fungi, or plant roots) could be distinguished within this broader subcommunity (Table 9.2). Similarly, individual plant species represent resource bases for relatively discrete component communities of associated arthropods and other organisms in the above-ground subcommunity (Curry 1994). Resource-based component communities are

TABLE 9.2 The proportion of energy and nitrogen derived from the bacteria, fungal, and root (including mycorrhizal fungi) resource channels by different faunal groups in the North American shortgrass steppe.

	Resource Channel		
Faunal Group	**Bacteria**	**Fungi**	**Roots**
Protozoa			
Flagellates	100	0	0
Amoebae	100	0	0
Ciliates	100	0	0
Nematodes			
Bacteriovores	100	0	0
Fungivores	0	90	10
Root-feeders	0	0	100
Omnivores	100	0	0
Predators	69	3	28
Microarthropods			
Mycophagous Collembola	0	90	10
Mycophagous oribatid mites	0	90	10
Mycophagous prostigmatid mites	0	90	10
Nematophagous mites	67	4	30
Predaceous mites	40	39	2

From J. Moore and Hunt (1988) by permission from Nature, © 1988 Macmillan Magazines, Ltd.

linked to each other by generalist herbivores and predators. Similarly, the canopy and soil/litter subcommunities are linked by species that feed above ground but pupate in the soil or feed on litter resources but disperse and bask on foliage and by predators and detritivores that move among substrates in search of resources.

The most inclusive approach to community description is represented by interaction webs, in which all species are connected by arrows indicating interactions. Relatively few communities are composed of sufficiently few species to depict all interactions conveniently. Hot springs and other communities subject to extreme abiotic conditions usually are composed of a few tolerant algal and invertebrate species (N.C. Collins *et al.* 1976). Communities composed of relatively few invertebrate and vertebrate species characterize some aquatic ecosystems (e.g., vernal pools, riffles, etc.). However, even the desert communities described by Polis (1991a) were composed of $>10^3$ arthropod species, most of which had not been studied sufficiently to provide complete information on interactions. A number of studies have addressed trophic interactions (i.e., food webs), although even trophic interactions are poorly known for many species, especially insects.

A number of techniques have been used to identify trophic relationships. Early studies of food web structure tracked radioisotopes through trophic exchanges (e.g., Crossley and Howden 1961). Stable isotopes or other tracers also can be tracked through feeding exchange (e.g., Christenson *et al.* 2002). Furthermore, animal tissues reflect the stable isotope ratios of their diet, with slight enrichment of ^{15}N with increasing trophic level (Blüthgen *et al.* 2003, Ponsard and Arditi 2000, Scheu and Falca 2000, Tayasu *et al.* 1997). However, interpretation of trophic interactions depends on the isotopic homogeneity of the diet (Gannes *et al.* 1997). Selective feeding on particular substrates can affect ^{13}C enrichment in animals (Šantrůčková *et al.* 2000). Adams and Sterner (2000) reported that ^{15}N enrichment was linearly related to dietary C:N ratio, which could vary sufficiently to indicate as much as a 2-trophic level separation, potentially leading to misidentification of trophic level for particular species.

Advances in molecular techniques have provided new tools for identifying interactions among species in communities. Enzyme-linked immunosorbent assay (ELISA) techniques involve development of antibodies against enzymes from potential food sources. These antibodies can be used to precipitate enzymes in gut samples containing the target food source. Irby and Apperson (1988) and Savage *et al.* (1993) used ELISA to identify associations between various mosquito species and their particular amphibian, reptile, bird, and mammal hosts. Agustí *et al.* (1999a) demonstrated the utility of this technique for detecting prey, *Helicoverpa armigera,* in heteropteran, *Dicyphus tamaninii, Macrolophus caliginosus,* and *Orius majusculus,* predator gut contents. More recently, polymerase chain reaction (PCR) and DNA amplification techniques have been used to illuminate feeding relationships (Suh *et al.* 2003). Broderick *et al.* (2004) used this methodology to describe the microbial community in gypsy moth, *Lymantria dispar,* midgut and to demonstrate that bacterial composition was influenced by the plant species composition of the diet. Agustí *et al.* (1999b), Y. Chen *et al.* (2000), Hoogendoorn and Heimpel (2001), and Zaidi *et al.* (1999) demonstrated that PCR and DNA amplification can be used to identify prey species in gut contents for 12–28 hours after predator feeding. Although these techniques can help identify feeding relationships, developing the sequence library to distinguish all potential prey in the field presents a challenge.

Several properties have appeared to characterize food webs (see Briand and Cohen 1984, Cohen and Palka 1990, Cohen *et al.* 1990, Martinez 1992, May 1983, Pimm 1980, 1982, Pimm and Kitching 1987, Pimm and Lawton 1977, 1980, Pimm and Rice 1987, Pimm *et al.* 1991, Polis 1991b, Reagan *et al.* 1996). However, food web analysis usually has been based on combination of all insects (often all arthropods) into a single category, in contrast to resolution at the individual species level for plants and vertebrates. Polis (1991b) and Reagan *et al.* (1996) increased the resolution of arthropod diversity to individual "kinds," based on taxonomy and similar phylogeny or trophic relationships, for evaluation of food web structure in desert and tropical rainforest communities, respectively. They found that the structure of their food webs differed from that of food webs in which arthropods were combined. Goldwasser and Roughgarden (1997) analyzed the effect of taxonomic resolution on food web structure and found that food web properties reflected the degree of taxonomic resolution. The following properties of food webs, based on analyses with insects or arthropods as a single category, are evaluated with respect to challenges based on greater resolution of arthropod diversity.

1. Food Chain Length

Early analyses indicated that the length of food chains within food webs should be relatively short, at most 3–5 links (May 1983, Pimm and Kitching 1987, Pimm and Lawton 1977), because the laws of thermodynamics predict energy limitation at higher trophic levels. Therefore, energy gain should be maximized by feeding lower on the food chain. At the same time, competition for prey is most severe at lower levels, perhaps restricting energy gains. Consequently, the trophic level selected by predators represents a tradeoff between maximizing energy availability and minimizing competition. However, Polis (1991b) and Reagan *et al.* (1996) found chain lengths of 6–19 links using food webs with greater resolution in arthropod taxonomy. Reagan *et al.* (1996) reported a mean chain length of 8.6, double the length of chains found when arthropods are combined into a single category.

2. Trophic Loops and Intraguild Predation

Loops, or reciprocal predation, in which two species feed on each other or a third species feeds on one and is eaten by the other, should be rare or absent because the size range of prey is constrained by physical limits and because loops potentially reduce population recovery following disturbance (Pimm 1982, Pimm and Rice 1987). Intraguild predation involves predation among members of the predator guild on each other. Cannibalism is considered a "self-loop" (see Fox 1975a).

Polis (1991b) and Reagan *et al.* (1996) reported the occurrence of a substantial number of loops, especially involving arthropods. In most cases, each species in the loop preys on juveniles of the other species. For example, in a tropical forest in Puerto Rico, adult centipedes prey on young frogs, whereas adult frogs prey on young centipedes. Polis (1991b) reported that several species of desert ants regularly prey on each other. Other predators constituted 9% of the overall diet of the aquatic heteropteran, *Notonecta hoffmanni,* studied by Fox (1975b). Longer loops involving up to four species have been observed (Reagan *et al.* 1996). Reagan *et al.* (1996) found that 35% of 19,800 observed chains (corrected to exclude loops) include at least one species involved in at least one loop.

Furthermore, a number of studies have demonstrated significant reduction in predator abundances as a result of intraguild predation (e.g., Denno *et al.* 2004, Erbilgin *et al.* 2004, Pérez-Lachaud *et al.* 2004, Rosenheim 2005). Rosenheim (2005) demonstrated through enclosure/exclosure experiments that abundance of the anthocorid bug, *Orius tristicolor,* was significantly reduced by intraguild predation by big-eyed bugs, *Geocoris* spp., and lacewing, *Chrysoperla* sp., larvae in cotton fields in California, United States, interfering with top-down control of spider mite, *Tetranychus* spp., prey. Reciprocal, or intraguild, predation may be pervasive within arthropod predator guilds, complicating measurement of food chain length and explaining irruptions of prey species when multiple predator species are present.

3. Food Web Connectance

Community connectance, the proportion of potential feeding relationships that actually occur in the community (Pimm 1982), should increase with increasing species richness as follows:

$$L = 0.14S^2 \tag{9.9}$$

where L is the number of links and S is the number of species (Martinez 1992). This *constant connectivity hypothesis* predicts that, on average, each species will be involved in predator–prey interactions with 14% of the other species in the community. Havens (1992) analyzed 50 pelagic food webs with species richness ranging from 10–74 and found that the number of links per species increased 4-fold over this range. Reagan *et al.* (1996) reported that the food web in a tropical forest in Puerto Rico supported constant connectance at low taxonomic resolution but that connectance dropped quickly as taxonomic resolution was increased. Polis (1991b) and Reagan *et al.* (1996) also found that the prediction that each species interacts with only 2–5 other species greatly underestimates the actual number of linkages per species and concluded that these properties are sensitive to taxonomic resolution.

4. Food Web Compartmentalization

Pimm and Lawton (1980) proposed that food webs should be compartmentalized between, but not within, habitats. Whereas the relatively distinct communities representing disturbed versus undisturbed patches within an ecosystem represent compartmentalization, the communities within habitat patches should not be compartmentalized. This property largely follows from the constant connectivity hypothesis (i.e., compartmentalization is inconsistent with equal linkage among species).

The vague definition of habitat complicates assessment of compartmentalization. For example, does soil/litter constitute a habitat or a subunit of the site habitat? Soil/litter subcommunities tend to be distinct from plant-based aboveground subcommunities.

Nevertheless, compartmentalization can be identified within recognized habitats. J. Moore and Hunt (1988), Polis (1991b), and Reagan *et al.* (1996) found distinct compartmentalization within the community of a single patch when arthropod species or "kinds" were distinguished (see Table 9.2). Distinct compartmentation of arthropod assemblages has been shown among plant species (e.g., Fig. 9.7) and even between trees and sapling of the same species (Basset 2001). Compartmentalization reflects the development of component communities composed of specialists feeding on particular resources and the resulting channels of energy and material transfer. Host specificity appears to occur more frequently and at a finer spatial scale among herbivorous and detritivorous arthropods, based on their small size, short life spans, and intricate biochemical interactions (see Chapter 3) that facilitate rapid adaptation for utilization of particular resources, even within individual leaves (e.g., Mopper and Strauss 1998, K. Parsons and de la Cruz 1980). Many parasitoids also are host specific, so that compartmentalization is maintained at higher trophic levels among arthropods. Of course, generalists at all trophic levels connect compartments and maintain the web of interactions. J. Moore and Hunt (1988) found that compartmentalized models of food webs were more stable than were noncompartmentalized webs.

5. *Omnivory*

Omnivores (defined as species feeding on more than one trophic level) should be rare (Pimm 1982, Pimm and Rice 1987). Pimm and Rice (1987) concluded that omnivory should reduce the stability of food web interactions. However, as noted earlier in the text, a number of studies have demonstrated intraguild predation (Denno *et al.* 2004, Erbilgin *et al.* 2004, Pérez-Lachaud *et al.* 2004, Rosenheim 2005), suggesting that top-down regulation of herbivore population irruptions could be disrupted when multiple predators are present. Polis (1991b) and Reagan *et al.* (1996) reported that omnivory is common in food webs when arthropods are resolved to species or "kinds." In fact, they found that most species fed at more than one trophic level, often from nonadjacent trophic levels, in desert and tropical rainforest communities.

Fagen (1997) tested the effect of omnivory on stability of community structure by manipulating the degree of omnivory (excluding either a specialist predator, the nabid bug, *Nabis alternatus,* or an omnivorous predator, wolf spiders, *Pardosa* spp.) in replicated plots, then disturbing the community by applying aphicide to disrupt prey, *Macrosiphum valeriani,* abundance. Plots with high levels of omnivory showed significantly reduced responses to disturbance for seven of 14 species, compared to plots with low levels of omnivory; no species showed significantly increased responses to disturbance. These data indicated that omnivory increased the stability of food web interactions.

6. *Ratio of Basal to Top Species*

Finally, ratios of species and links from basal to intermediate to top trophic levels (where basal species are prey only, intermediate species are prey and predators, and top predators have no predators) are expected to be constant (Briand and Cohen 1984). This implies a large proportion of top predators. Top predators are expected to comprise 29% of all species in a given community, and prey-to-predator ratios should be < 1.0 (Briand and Cohen 1984).

As shown for the properties discussed in the preceding text, this property reflects poor resolution of arthropod diversity. Top predators appear to be common because they are easily distinguished vertebrate species, whereas poor taxonomic resolution at basal and intermediate levels underrepresents their diversity. Reagan *et al.* (1996) reported that in a rainforest food web, which distinguished "kinds" of arthropods, representation of basal and intermediate species was 30% and 70% of all species, respectively, and the proportion of top predators was < 1%. Polis (1991b) also reported that top predators were rare or absent in desert communities. Both Polis (1991b) and Reagan *et al.* (1996) reported that ratios of prey species to predator species are much greater than 1.0 when the true diversity of lower trophic levels is represented.

Although the properties of food webs identified by early theorists may be flawed to the extent that arthropod diversity has not been resolved adequately, they represent hypotheses that have stimulated considerable research into community organization. Future advances in food web theory will reflect efforts to address arthropods at the same level of taxonomic resolution as other taxa.

C. Functional Organization

A third approach to community description is based on the guild, or functional group, concept (Cummins 1973, Hawkins and MacMahon 1989, Körner 1993, Root 1967, Simberloff and Dayan 1991). The guild concept was originally proposed by Root (1967), who defined a guild as a group of species, regardless of taxonomic affiliation, that exploit the same class of environmental resources in a similar way. This term has been useful for studying potentially co-evolved species that compete for, and partition use of, a common resource. The largely equivalent term, functional group, was proposed by Cummins (1973) to refer to a group of species having a similar ecological function. Insects, as well as other organisms, have been combined into guilds or functional groups based on similarity of response to environmental conditions (e.g., Coulson *et al.* 1986, Fielding and Brusven 1993, Grime 1977, Root 1973) or of effects on resources or ecosystem processes (e.g., Romoser and Stoffolano 1998, Schowalter *et al.* 1981c, Siepel and de Ruiter-Dijkman 1993). This method of grouping is one basis for pooling "kinds" of organisms, as discussed in the previous section.

Pooling species in this way has been attractive for a number of reasons (Root 1967, Simberloff and Dayan 1991). First, it reflects the compartmentalization of natural communities (see previous section) and focuses attention on sympatric species that share an ecological relationship (e.g., competing for a resource or affecting a particular ecological process), regardless of taxonomic relationship. Second, it helps resolve multiple usage of the term "niche" to refer both to the functional role of a species and the set of conditions that determines its presence in the community. Use of guild or functional group to refer to species' ecological role(s) permits limitation of the term niche to refer to the conditions that determine species presence. Third, this concept facilitates comparative studies of communities that may share no taxa but do share functional groupings (e.g., herbivores, pollinators, detritivores, etc.). Guild or functional groupings permit focus on a particular group, with specific functional relationships, among community types. Hence, researchers avoid the necessity of cataloging and studying all species represented in the community, a nearly impossible task, before comparison is possible. Functional groupings are particularly useful for simplifying ecosystem models to emphasize effects of functional groups with particular patterns of carbon and nutrient use on fluxes of energy and matter. Nevertheless, this method for describing communities has been used more widely among aquatic ecologists than among terrestrial ecologists.

The designation of functional groupings is largely a matter of convenience and depends on research objectives (e.g., Hawkins and MacMahon 1989, Körner 1993, Simberloff and Dayan 1991). For example, defining "same class of resources" or "in a similar manner" is ambiguous. Each species represents a unique combination of abilities to respond to environmental conditions and to affect ecosystem processes (i.e., species within functional groups are similar only on the basis of the particular criteria used to distinguish the groups). Characterization of functional groups based on response to climate change, response to a disturbance gradient, effect on carbon flux, or effect on biogeochemical cycling would involve different combinations of species.

Insects are particularly difficult to categorize because functional roles can change seasonally (wasps switching between predation and pollination) or during maturation (e.g., sedentary herbivorous larvae becoming mobile pollinating adults, aquatic larvae becoming terrestrial adults, etc.), and many species are too poorly known to assign functional roles. All Homoptera can be assigned to a plant sap-sucking functional group, but various species would be assigned to different functional groups on the basis of the plant part(s) affected (e.g., foliage, shoots, or roots, xylem or phloem). Clearly, functional groups can be subdivided to represent a diversity of responses to different gradients or subtle differences in ecological effects. For example, a stress-adapted "functional group" could be divided into subgroups that tolerate desiccation, physiologically prevent desiccation, or avoid desiccation by feeding on plant fluids. Similarly, a foliage-feeder guild can be divided into subgroups that fragment foliage, mine foliage, or suck cellular fluids; feed on different plant species; etc., each subgroup affecting energy and matter fluxes in a different manner. Luh and Croft (1999) developed a computer algorithm to classify predaceous phytoseiid mite species into functional groups (specialist vs. generalist predators). The computer-generated classification confirmed the importance of the combination of life history traits used previously to distinguish functional groups.

Species included in a particular functional group should not be considered redundant (Beare *et al.* 1995, Lawton and Brown 1993), but rather complementary, in terms of ensuring ecological functions. Schowalter *et al.* (1999) reported that each functional group defined on the basis of feeding type included species that responded positively, negatively, or nonlinearly to moisture availability. Species replacement within functional groups maintained functional organization over an experimental moisture gradient.

Changes in the relative abundance or biomass of functional groups can signal changes in the rate and direction of ecological processes. For example, changes in the relative proportions of filter-feeder versus shredder functional groups in aquatic ecosystems affect the ways in which detrital resources are processed within the stream community and their contribution to downstream communities. Similarly, changes in the relative proportions of folivores versus sap-suckers affect the flux of nutrients as solid materials versus liquid (e.g., honeydew) and their effect on the detrital community (e.g., Schowalter and Lowman 1999, Stadler and Müller 1996, Stadler *et al.* 1998).

The functional group concept permits a convenient compromise in dealing with diversity (i.e., sufficient grouping to simplify taxonomic diversity while retaining an ecologically relevant level of functional diversity). Therefore, the functional group approach has become widely used in ecosystem ecology.

II. PATTERNS OF COMMUNITY STRUCTURE

A central theme of community ecology has been identification of patterns in community structure across environmental gradients in space and time (see also Chapter 10). The diversity of community types at landscape and regional scales has been a largely neglected aspect of biodiversity but is important to the maintenance of regional species pools and metapopulation dynamics for many species. In addition, the mosaic of community types on a landscape may confer conditional stability to the broader ecosystem, in terms of relatively consistent proportions of community types over time (see Chapters 10 and 15).

Identification of patterns in community organization has become increasingly important to population and ecosystem management goals. Introduction of exotic insects to combat noxious pests (weeds or other insects) requires attention to the ability of the biocontrol agent to establish itself within the community and to its potential effects on nontarget components of the community. Efforts to conserve or restore threatened species require consideration and maintenance of the underlying community organization.

Depending on the descriptive approach taken (see earlier in this chapter), patterns have been sought in terms of species diversity, food web structure, or guild or functional group composition. Unfortunately, comparison of data among communities has been hampered by the different approaches used to describe communities compounded by the variety of sampling techniques, with their distinct biases, used to collect community data. For example, sweep netting, light trapping, interception trapping, pitfall trapping, soil coring, canopy fumigation, and branch bagging are among the techniques commonly used to sample terrestrial arthropods (Leather 2005). These techniques differ in their representation of nocturnal versus diurnal flying insects, arboreal versus soil/litter species, and sessile versus mobile species, etc. (e.g., Blanton 1990, Leather 2005, Majer and Recher 1988, Southwood 1978). Relatively few studies have used the same, or similar, techniques to provide comparative data among community types or locations. Some proposed patterns have been challenged as subsequent studies provided more directly comparable data or increased resolution of arthropod taxonomy (e.g., Hawkins and MacMahon 1989, Polis 1991b, Reagan *et al.* 1996). Disturbance history, or stage of postdisturbance recovery, also affects community structure (e.g., Harding *et al.* 1998, Schowalter *et al.* 2003, E. Wilson 1969; see Chapter 10). However, the history of disturbance at sampled sites often is unknown, potentially confounding interpretation of differences in community structure. Nevertheless, apparent patterns identified at a variety of spatial scales may serve as useful hypotheses to guide future studies.

A. Global Patterns

Communities can be distinguished on a taxonomic basis at a global scale because of the distinct faunas among biogeographic realms (A. Wallace 1876). However, similar community types on different continents often are dominated by unrelated species with similar attributes, termed *ecological equivalence.* For example, grassland communities on every continent should show similar food web structure and functional group organization, reflecting similar environmental conditions, regardless of taxonomic representation. A number of studies have indicated global patterns in community structure related to latitudinal gradients in temperature and moisture and to the ecological history of adaptive radiation of particular taxa.

Latitudinal gradients in temperature and precipitation establish a global template of habitat suitability, as discussed in Chapters 2 and 7. Equatorial areas, characterized by high sun angle and generally high precipitation, provide favorable conditions of light, temperature, and moisture, although seasonal patterns of precipitation in some tropical areas create periods of adverse conditions for many organisms. The strongly seasonal climate of temperate zones requires specific adaptations for survival during seasonally unfavorable conditions, thereby limiting species diversity. The harsh conditions of temperate deserts and high-latitude zones generally restrict the number of species that can be supported or that can adapt to these conditions.

Species richness generally decreases with latitude for a wide variety of taxa (Price 1997, J. Stout and Vandermeer 1975, Willig and Lyons 1998). This gradient may be particularly steep for insects, which would be expected to show increasing species richness toward warmer latitudes, but may not be reflected by all taxa (e.g., aphids, Dixon 1985) or component communities (Vinson and Hawkins 1998). Vinson and Hawkins (1998) reviewed literature for stream communities and concluded that species richness is highly variable and no strong latitudinal trends are apparent.

Some studies suggest that the tropics may support several million new arthropod species (Erwin 1995, May 1988, E. Wilson 1992). Global arthropod diversity currently is estimated at 4–6 million species, with most species in the tropics (Novotný *et al.* 2002). Although diversity may be high in the tropics, densities may be low and make detection of many species difficult.

Although increasingly favorable climate toward the equator is an attractive explanation for the observed trend in diversity, several alternative hypotheses have been proposed. Terborgh (1973) showed that the apparent trend in species richness with latitude may reflect increasing land area toward the equator. He noted that climate is relatively constant across a wide belt between 20°N and S latitudes but shows a distinct latitudinal gradient above 20°N and S latitudes. Combining climate and surface area gradients yielded a latitudinal gradient in habitat area available within each climate class, with a preponderance of global surface area in tropical habitat. These data suggest that gradients in species richness reflect habitat area available for within-habitat speciation (see discussion later in this chapter).

Latitudinal gradients in species richness also may reflect greater primary productivity in the tropics (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Waide *et al.* 1999; see later in this chapter). Furthermore, Willig and Lyons (1998) showed that latitudinal gradients can result from chance.

Superimposed on the latitudinal gradients are the relatively distinct biogeographic realms identified by A. Wallace (1876). These biogeographic realms reflect the history of continental breakup, with southern floras and faunas largely distinct from northern floras and faunas (see Chapter 7). However, the southern continents show a varied history of reconnection with the northern continents that has resulted in invasion primarily by northern species. The proximity of North America and Eurasia has facilitated movement of species between these land masses, leading to development of a Holarctic species component, especially within the arctic and boreal biomes. Whereas many genera, and even some species, occur throughout the Holarctic realm, the flora and fauna of Australia have remained relatively distinct as a result of continued isolation.

Species richness also may be related to geologic time. E. Wilson (1969) suggested that co-evolution should improve the efficiency of total resource exploitation and lead to further increase in co-existing species over time. In other words, a habitat or resource that has persisted for a longer period of time would acquire more species than a more recently derived habitat or resource. Birks (1980) found that the residence time of tree species in Britain was strongly correlated with the diversity of associated insect species. Tree species that had a longer history of occurrence in Britain hosted a larger number of species than did tree species with shorter residence times. Again, because residence time is correlated with area of occurrence (habitat area), the effects of these two factors cannot be distinguished easily (Price 1997; see later in this chapter).

B. Biome and Landscape Patterns

Patterns in species richness, food web structure, and functional organization have been observed among biomes and across landscapes. To some extent, patterns may reflect variation in occurrence or dominance of certain taxa in different biomes. Regional species pools may obscure effects of local habitat conditions on species richness (Kozár 1992a), especially in temperate ecosystems (Basset 1996), but few ecologists have addressed the extent to which the regional species pool may influence local species richness. Gering *et al.* (2003), Kitching *et al.* (1993), and Progar and Schowalter (2002) distinguished arthropod assemblages among sites within biomes that reflected regional gradients in environmental conditions. Various hypotheses have been proposed to account for apparent patterns at the biome and landscape level (e.g., Price 1997, Tilman and Pacala 1993). However, as more data have become available, some patterns have become equivocal.

General functional groups are common to all biomes (e.g., grazing herbivores [depending on degree of autochthonous primary production in streams], predators, parasites, and detritivores), whereas other functional groups depend on particular resources being present (e.g., sap-suckers require vascular plants and wood borers require wood resources). Proportions of the fauna representing different functional groups vary among biomes. Low-order streams have primarily detrital-based resources, and their communities are dominated by detritivores and associated predators and parasites. Other communities represent various proportions of autotroph functional groups (e.g., chemoautotrophs, ruderal, competitive, and stress-tolerant vascular vs. nonvascular plants) and heterotroph functional groups (herbivores, predators, detritivores) (see Chapter 11).

Different species compose these functional groups in different biomes. For example, the insect grazer functional group is composed primarily of moths, beetles, and tree crickets in broadleaved forests, moths and sawflies in coniferous forests (Schowalter 1995, Schowalter and Ganio 1999, Schowalter *et al.* 1981c), grasshoppers in grasslands and shrublands (Curry 1994), and caddisflies and flies in aquatic communities (e.g., Hart 1992). The predator functional group in terrestrial arthropod communities is dominated by a variety of arachnids, beetles, flies, and wasps, whereas in aquatic arthropod communities this functional group is dominated by dragonflies, true bugs, and beetles.

Among terrestrial biomes, species richness generally is assumed to increase from harsh biomes (e.g., tundra and desert) to grassland to forest, again reflecting differences in physical complexity, suitability, and stability of the habitat (Bazzaz 1975, Tilman and Pacala 1993). However, this trend is not apparent for arthropods among communities where extensive species inventories are available (e.g., Table 9.1). Species richness is not always linearly related to primary productivity and patterns likely depend on scale (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Waide *et al.* 1999). Species richness often declines above intermediate levels of productivity, perhaps because more productive communities are dominated by larger individuals that reduce habitat heterogeneity or because more productive and stable communities favor competitive exclusion of some species by the best adapted species (Tilman and Pacala 1993). For example, continuous fertilization of permanent pasture at Rothamsted, United Kingdom, since 1856 resulted in changes in species rank-abundance pattern from a log normal curve in 1856 to progressively more geometric curves by 1949 (see Fig. 9.3) (Kempton 1979).

Functional group composition has not shown consistent differences among biomes (Hawkins and MacMahon 1989, Stork 1987). Detritivores represent a relatively greater proportion of the community in boreal forests, headwater streams, and other biomes characterized by accumulated organic material and a lower proportion in tropical forests, deserts, and other biomes with little organic matter accumulation (Haggerty *et al.* 2002, Seastedt 1984). Wood borers occur only in forest or shrub ecosystems with abundant wood resources. Pollinators are more diverse in tropical forests and deserts where plant diversity and isolation have led to greater reliance on insect and vertebrate pollinators, compared to temperate grassland and forest and arctic biomes. Proportional representation of species and individuals among functional groups varies widely among canopy arthropod communities in temperate and tropical forests, depending on tree species composition (Fig. 9.8) (V. Moran and Southwood 1982, Schowalter and Ganio 1998, 1999, Stork 1987).

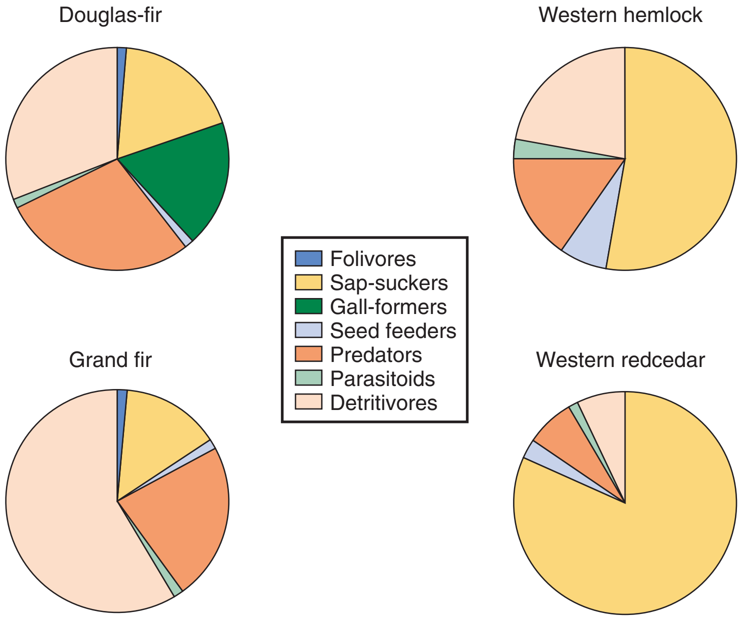


FIG. 9.8 Functional group organization of arthropod communities in canopies of four old-growth conifer species at the Wind River Canopy Crane Research Facility in southwestern Washington. Data from Schowalter and Ganio (1998).

At the landscape or drainage basin scale, patterns in species richness and functional group organization can be related to local variation in physical conditions. The history and geographic pattern of disturbance may be particularly important factors affecting variation in community structure. Polis *et al.* (1997a) concluded that the movement of organisms and resources among the interconnected community types composing a landscape can contribute to the organization of the broader landscape community by subsidizing more resource-limited local communities. However, Basset (1996) found that diversity in tropical rainforest trees was related to five factors: numbers of young leaves available throughout the year, ant abundance, leaf palatability, leaf water content, and altitudinal range. These data suggested that local factors may be more important determinants of local species diversity and community structure in complex ecosystems, such as tropical forests, than in less complex ecosystems, such as temperate forests.

Diversity of stream insects varies among riffle and pool habitats and substrate conditions (Ward 1992). Diversity generally is higher in running water with cobble substrates, with high oxygen supply and heterogenous structure, than in standing water with mud, sand, or gravel substrates.

Vinson and Hawkins (1998) found six studies that compared species richness of stream insects over drainage basins. Species diversity varied with elevation, which co-varied with a number of important factors, such as stream morphology, flow rate and volume, riparian cover, and agricultural or urban land use. In one study Carter *et al.* (1996) used multivariate analysis (TWINSPAN) to compare species composition among 60 sites representing first-order (characterized by narrow V-shaped channel, steep gradient, nearly complete canopy cover) to sixth-order (characterized by wide channel, low gradient, little canopy cover) streams over a 15,540 km^2 drainage basin. They identified five communities distinguished largely by elevation. The highest species richness occurred in mid-order, mid-elevation streams that included species groups characterizing both higher- and lower-order streams.

Transition zones (ecotones) between community types usually have higher species richness because they include species from each of the neighboring communities. Zhong *et al.* (2003) reported that adult mosquito species diversity was higher at sites surrounded by freshwater and salt marsh than at sites surrounded by either freshwater or salt-marsh alone. Ecotones can move across the landscape as environmental conditions change. For example, the northern edge of Scots pine, *Pinus sylvestris,* forest in Scotland moved rapidly 70–80 km northward about 4000 years BP then retreated southward again about 400 years later (Gear and Huntley 1991). Sharp edges between community types, such as result from land-use practices, reduce the value of this ecotone as a transition zone.

Patches representing different stages of postdisturbance recovery show distinct patterns of species richness, food web structure, and functional group organization (see Marquis et al. 2002, Chapter 10). Species richness usually increases during community development up to an equilibrium, perhaps declining somewhat prior to reaching equilibrium (e.g., MacArthur and Wilson 1967, E. Wilson 1969). As the number of species increases, the number of species interactions increases. Food chains that characterize simpler communities develop into more complex food webs (E. Wilson 1969). Schowalter (1995), Schowalter and Ganio (1999), and Schowalter *et al.* (1981c) found that patches of recently disturbed temperate and tropical forests were characterized by higher sap-sucker/folivore ratios than were patches of undisturbed forests, even when data were reported as biomass.

Shure and Phillips (1991) reported that species richness and functional group composition are modified by patch size (see Fig. 6.5). Species richness was lowest in mid-sized canopy openings (0.08–0.4 ha). Herbivore guilds generally had lowest biomass in mid-sized canopy openings; omnivore biomass peaked in the smallest openings (0.016 ha) and then declined as opening size increased; predator biomass was highest in the control forest and smallest openings and lowest in the mid-sized openings; and detritivore biomass was similar among most openings but much lower in the largest openings (10 ha). This pattern may indicate the scale that distinguishes communities characterizing closed-canopy and open-canopy forest. Smaller openings were influenced by surrounding forest, whereas larger openings favored species more tolerant of exposure and altered plant conditions (e.g., early successional species and higher phenolic concentrations) (Dudt and Shure 1994, Shure and Wilson 1993). Intermediate-sized openings may be too exposed for forest species but insufficiently exposed for earlier successional species. However, species richness generally increases with habitat area (Fig. 9.9) (M. Johnson and Simberloff 1974, MacArthur and Wilson 1967) for reasons discussed in the next section.

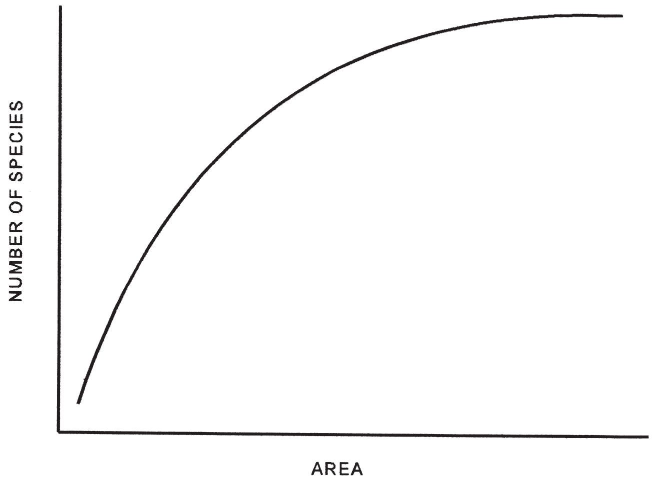


FIG. 9.9 Relationship between species richness and geographic area.

III. DETERMINANTS OF COMMUNITY STRUCTURE

A number of factors affect community structure (e.g. Price 1997). Factors associated with habitat area, resource availability, and species interactions appear to have the greatest influence.

A. Habitat Area and Complexity

The relationship between number of species and sampling effort, in time or space, has been widely recognized and supported (He and Legendre 2002). The increase in number of species with increasing number of samples reflects the greater representation of the community. Similarly, a larger habitat area will "sample" a larger proportion of a regional species pool (Summerville and Crist 2004). Increasing habitat area also tends to represent increasing heterogeneity of habitat conditions (e.g., M. Johnson and Simberloff 1974, D. Strong *et al.* 1984), providing an increasing number of niches.

In developing the *Theory of Island Biogeography,* MacArthur and Wilson (1967) emphasized the relationship between species richness (S) and island area (a), expressed as follows:

$$S = Ca^{z} \tag{9.10}$$

where C depends on the taxon and biogeographic region and z is a parameter that varies little among taxa or biogeographic regions, generally falling in the range of 0.20–0.35 (see Fig. 9.9). The value of z increases with habitat heterogeneity and proximity to the mainland. For nonisolated sample areas within islands or within continental areas, the relationship between species number and sample area is similar, but z is smaller, generally 0.12–0.17 (MacArthur and Wilson 1967).

Habitat area has continued to be viewed as a primary factor affecting species richness, likely influencing apparent gradients in species richness with latitude and host residence time (e.g., Birks 1980, Price 1997, Terborgh 1973), as discussed earlier in this chapter. However, habitat area also is a surrogate for habitat heterogeneity. Larger islands are more likely than smaller islands to represent a wider range in elevation, soil types, aspects, etc. Similarly, larger continental areas are more likely than smaller areas to represent a range of habitat conditions. Because relatively distinct component communities develop on particular resources, such as plant or microbial species (e.g., J. Moore and Hunt 1988), species richness increases exponentially as representation of resource diversity increases. Furthermore, habitat heterogeneity provides for refuges from competition or predation (i.e., local patches of competition- or predator-free space). The architectural complexity of individual plants also can affect the diversity of associated fauna (Lawton 1983).

Fragmentation of habitat types often alters species richness and other measures of diversity. Larger fragments retain a greater proportion of species richness than do smaller fragments (Fig. 9.10) (Collinge 2000, Kruess and Tscharntke 2000, Summerville and Crist 2004). Species characteristic of the fragmented habitat often are replaced by species characterizing the surrounding matrix (e.g., Summerville and Crist 2004). Some guilds may be more sensitive to fragmentation than are others. Golden and Crist (1999) reported that sap-sucking herbivores and parasitoids were significantly reduced by fragmentation of a goldenrod community, but chewing herbivores and predators were largely unaffected. Overall insect species richness was reduced by fragmentation, primarily through loss of rare species.

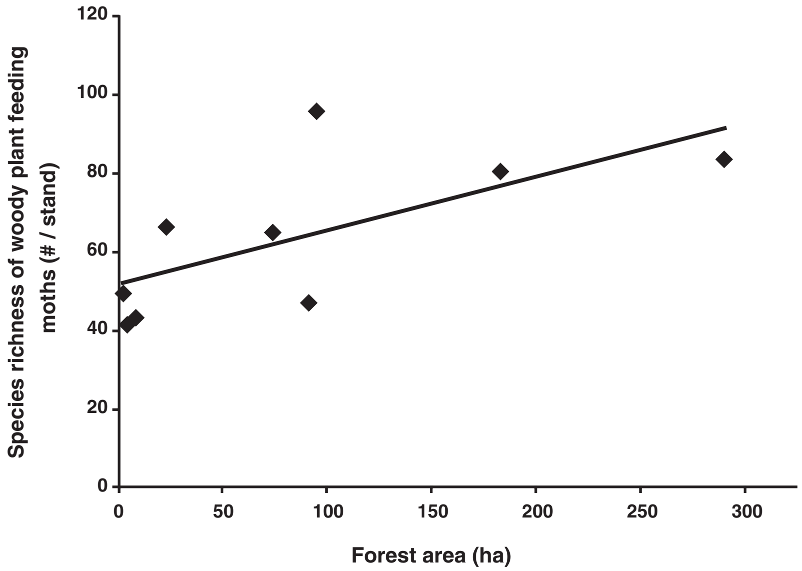


FIG. 9.10 Significant ($P < 0.05$, $R^2 = 0.61$) relationship between the size of forest fragments and number of woody-plant-feeding moth species in the western Allegheny Plateau of eastern North America. From Summerville and Crist (2004) with permission from Ecography. Please see extended permission list pg 571.

B. Habitat Stability

Habitat stability determines the length of time available for community development (see Chapter 10). E. Wilson (1969) proposed four stages in community development. The *noninteractive stage* occurs on newly available habitat or immediately following a disturbance, when numbers of species and population sizes are low. As species number rises during the *interactive stage,* competition and predation influence community structure, with some species disappearing and new species arriving. The *assortative stage* is characterized by persistence of species that can co-exist and utilize resources most efficiently, facilitating species packing. Finally, the *evolutionary stage* is characterized by co-evolution that increases the efficiency of overall utilization and species packing. Community development in frequently disturbed habitats cannot progress beyond earlier stages, whereas more stable habitats permit advanced community development and increased species richness. However, the most stable habitats also allow the most adapted species to preempt resources from other species, leading to a decline in species richness (see the following sections). This trend has led to the development of the *intermediate disturbance hypothesis,* which predicts that species richness peaks at intermediate levels of disturbance (e.g., Connell 1978, Sousa 1985, but see Reice 1985). Community recovery from disturbance is described more fully in Chapter 10.

C. Resource Availability

As discussed earlier in this chapter, the availability of particular resources determines the presence of associated species. If a limiting resource (host) becomes more abundant, then associated species also become more abundant until some other factor(s) become limiting. For example, Siemann (1998) reported that experimental fertilization of grassland plots increased arthropod species richness and abundance (Fig. 9.11).

Limiting resources may preclude any single adaptive strategy from becoming dominant and thereby maintain high species richness. Rosenzweig and Abramsky (1993), Tilman and Pacala (1993), and Waide *et al.* (1999) concluded that species richness is not always linearly related to productivity. Intermediate levels of productivity often support the highest diversity because higher productivity favors dominance by the most competitive species. Mittelbach *et al.* (2001) compiled 171 published studies relating species richness and productivity for aquatic and terrestrial plants and animals. Hump-shaped relationships were most common, indicating that productivity generally was higher at intermediate levels of species richness.

A number of studies have compared species richness between relatively homogeneous and heterogeneous environments (e.g., Cromartie 1975, Risch 1980, 1981, Root 1973, D. Strong *et al.* 1984, Tahvanainen and Root 1972). Because organisms have greater difficulty maintaining energy and nutrient balance when resources are scattered (see Chapter 4), the abundance of individual species generally decreases with increasing resource heterogeneity, precluding exclusive use

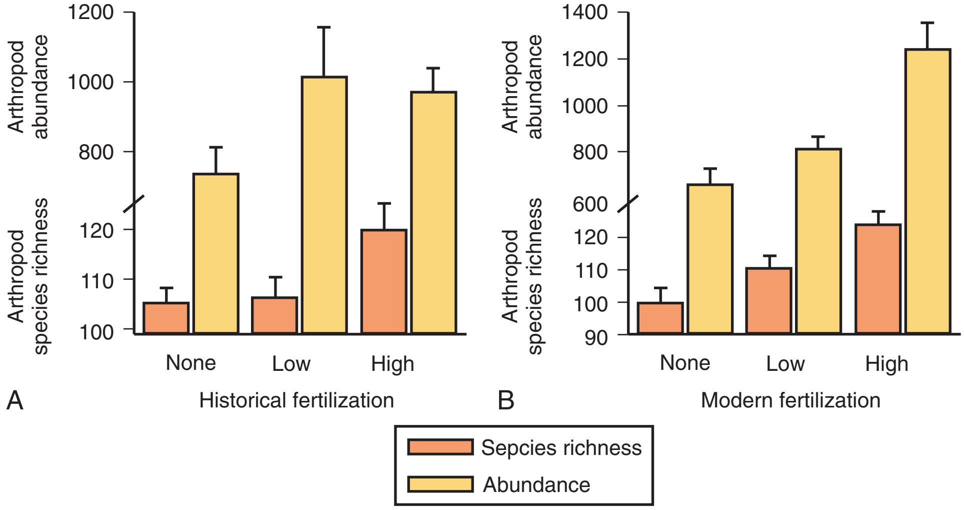


FIG. 9.11 Responses of arthropod species richness and abundance to historical (*a*) and experimental (*b*) fertilization treatments. Vertical lines represent 1 SE. From Siemann (1998) with permission from the Ecological Society of America. Please see extended permission list pg 571.

of the niche and permitting species richness to increase. By contrast, homogeneous resources facilitate rise to competitive dominance by the best-adapted species, leading to reduced species richness. Extensive planting of agricultural or silvicultural monocultures establishes the conditions necessary for some species to reach epidemic population levels across landscapes (see Chapter 7), reducing availability of resources shared with other species but providing prey resources for predators (Polis *et al.* 1997a; see also Chapter 8).

D. Species Interactions

Species interactions can enhance or preclude persistence of some species, as discussed in Chapter 8. As noted in the preceding text, species populations cannot persist where their host species are absent. However, the presence of competitors, predators, and mutualists also affects persistence of associated species, both directly and indirectly. In the past, species interactions often were viewed as evidence of co-evolution. However, species colonizing new areas can occupy niches through preconditioning or left vacant by extinction (Diamond 1990, Janzen and Martin 1982, Janzen 1985). For example, introduced species often become successfully established in their new habitats without benefit of co-evolution. Nevertheless, their presence in the community shapes environmental conditions that affect subsequent adaptations. S. Gould and Vrba (1982) proposed the term "exaptation" to describe characters evolved for other purposes but that "preadapt" an organism for current conditions.

Some species can have particularly profound effects on community structure. Their presence in a community leads to a different community structure than occurs in their absence. A top predator that preferentially preys on the most abundant of several competing prey species can prevent any single species from competitively suppressing others. R. Paine (1966, 1969a, b) considered such species to be *keystone species.* Bond (1993) and Power *et al.* (1996) applied this term to any species that has effects on ecosystem structure or function that are disproportionate to their abundance or biomass.

Some insect species could be considered to be keystone species to the extent that their abundance greatly alters diversity, productivity, rates of energy or nutrient flux, etc. Many herbivorous insects increase the diversity of plant species by selectively reducing the density of abundant host species and providing space and resources for nonhost plants (Lawton and Brown 1993, Schowalter and Lowman 1999). The southern pine beetle, *Dendroctonus frontalis,* is capable, at high population densities, of killing pine trees and increasing the availability of woody resources that maintain populations of other xylophagous species (Flamm *et al.* 1993). Naiads of the large dragonfly, *Tramea lacerata,* prey on other dragonflies as well as on various other taxa that also are prey of other dragonfly and damselfly naiads. Wissinger and McGrady (1993) found that addition of *T. lacerata* to wetland communities had a direct negative effect on damselfly prey but also an indirect positive effect through reduced numbers of other predaceous dragonflies. Termites and ants affect soil structure and fertility in ways that determine vegetation development (see Chapters 13 and 14).

As discussed in Chapter 6, the combination of bottom-up (resource supply) and top-down (trophic cascades) factors tends to stabilize population levels. Changes in abundance of any trophic level, however, affect abundances at other trophic levels. Generally, increased abundance at one trophic level increases resources available to the next higher trophic level, increasing abundance at that level but reducing abundance at the next lower level. Reduced abundance at the lower trophic level reduces its control over the second lower trophic level, which increases in abundance and reduces abundance at the third lower trophic level.

Such trophic cascades are commonly observed in aquatic ecosystems (Batzer *et al.* 2000b, Carpenter and Kitchell 1984, 1987, 1988, Vanni and Layne 1997). Fewer examples of trophic cascades controlled by top predators have been observed in terrestrial ecosystems. M. Hunter *et al.* (2003) reported that exclusion of litter predators in litterbags increased Collembola abundances and litter decomposition rate.

Letourneau and Dyer (1998) and L. Dyer and Letourneau (1999a, b) described a trophic cascade in a neotropical rainforest community. Clerid beetle, *Tarsobaenus letourneauae,* predation on ants, especially *Pheidole bicornis,* reduced ant abundance and increased herbivore abundance and herbivory on *Piper cenocladum* ant plants. Where this beetle was absent and spiders were a less effective top predator, ant abundance was higher and reduced herbivore abundance (Fig. 9.12). Manipulation of top-down and bottom-up effects indicated that increased resources (light and nutrients) directly increased plant biomass but had no indirect effect on predators or top predators, but ant exclusion indirectly affected plant biomass by increasing herbivory (Dyer and Letourneau 1999a).

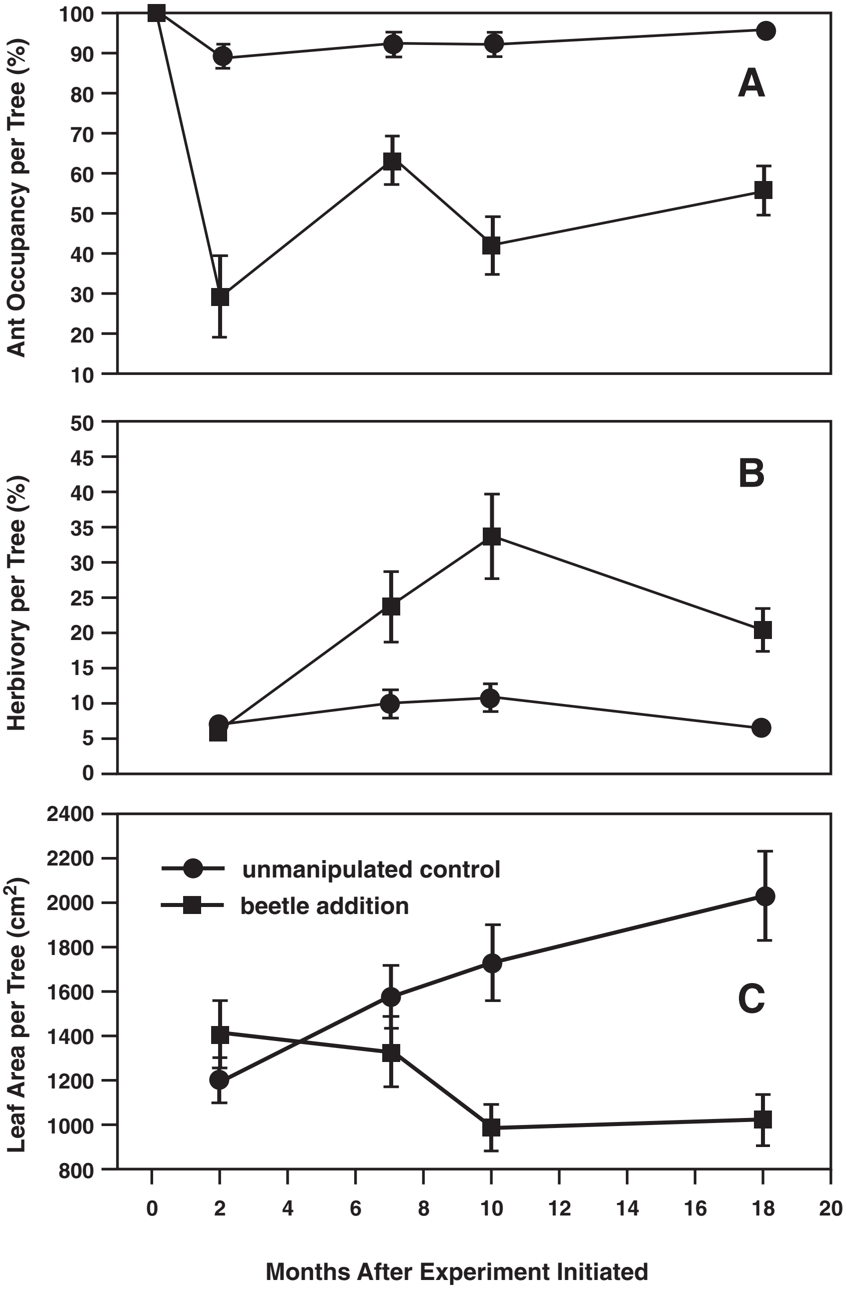


FIG. 9.12 Mean ant abundance (percentage of occupied petiole chambers per plant), mean folivory (leaf area eaten per *Piper cenocladum* shrub), and mean leaf area per shrub before (0–2 months) and after (7–18 months) addition of a top predator, *Tarsobaenus* beetles, to half the shrubs. Vertical bars represent 1 SE. From L. Dyer and Letourneau (1999) with permission from the National Academy of Sciences.

Linkages between communities can affect trophic cascades. Terrestrial arthropod inputs to aquatic systems provide a resource subsidy that influences predator–prey interactions. Nakano *et al.* (1999) experimentally manipulated terrestrial arthropod inputs and predatory fish presence in forest headwater streams in northern Japan. When terrestrial arthropod inputs were reduced, predatory fish switched from terrestrial to aquatic arthropod prey, reducing aquatic arthropod abundance and increasing periphyton biomass. By contrast, removal of predatory fish did not significantly alter the food web, indicating that the trophic cascade was controlled by terrestrial arthropod inputs. Such linkages control fluxes of energy and nutrients between ecosystems.

IV. SUMMARY

Communities are composed of the species occupying a site. Identification of patterns in community structure has been a major goal of ecological research. However, no standard approach for delimiting a site and describing or comparing community structure has been adopted. Indices of species diversity, food web structure, and functional group organization are three methods used to facilitate comparison among communities.

Species diversity has two components: richness and evenness. Richness is the number of species in the community, whereas evenness is a measure of relative abundances. These two components can be represented by rank-abundance curves and by diversity indices. Geometric rank-abundance curves characterize harsh or disturbed habitats with a limited number of adapted species and strong dominance hierarchy, whereas log and broken stick models characterize more stable habitats with higher species accumulation and greater evenness in abundance among species. A number of diversity indices and similarity indices have been developed to integrate richness and evenness in a variable that can be compared among community types.

Food web structure represents the network of pairwise interactions among the species in the community. A number of food web attributes have been proposed, based on limited taxonomic resolution of insects and other arthropods. These hypotheses are being challenged as greater resolution of arthropod taxonomy reveals networks of interactions within this diverse group.

Functional group organization reflects combination of species on the basis of functional responses to environmental variables or effects on ecological processes, regardless of taxonomic affiliation. This approach has become popular because it simplifies species diversity in an ecologically meaningful way. However, the allocation of species to functional groups is based on particular objectives and is therefore arbitrary to the extent that each species represents a unique combination of functional responses or effects.

The noncomparable descriptions of communities based on these three approaches, compounded by the variety of arthropod sampling techniques, each with its unique biases, have hindered comparison of community structure among habitat types. Many taxa show latitudinal gradients in abundance, with species richness increasing toward the equator. However, the climate gradient thought to underlie this trend is correlated with latitudinal gradients in habitat area and productivity. Some taxonomic groups are more diverse within biogeographic realms of origin or where resources have been available over longer time periods. Some functional groups are more abundant in certain biomes (e.g., pollinators in diverse tropical habitats and detritivores and wood borers in habitats with greater organic matter or wood accumulation).

Habitat area and stability, resource availability, and species interactions are major factors that affect community structure. Habitat area affects the pool of species available and the heterogeneity of habitat conditions and resources. Habitat stability determines the length of time available for species accumulation, assortment, and species packing. Species richness generally increases with resource availability, up to a point at which the most adapted species competitively suppress other species. Species interactions often affect persistence in a particular habitat. Colonists cannot survive unless their host resources are available. Competition, predation, and mutualism also affect species directly and indirectly. Indirect effects often are at least as important as direct effects. Keystone species have effects on community structure or ecosystem processes that are disproportionate to their numbers or biomass. Keystone species include predators that focus on the most abundant prey species, thereby reducing competition among prey species and maintaining more species than would co-exist in the absence of the predator. Some herbivorous insects function as keystone species by selectively reducing abundance of dominant host species and facilitating persistence of nonhosts. Trophic cascades reflect top-down effects of predators reducing prey abundance, thereby increasing abundance of the trophic level supporting the prey.

10

Community Dynamics

COMMUNITY STRUCTURE CHANGES THROUGH TIME AS SPECIES abundances change, altering the network of interactions. Short-term (e.g., seasonal or annual) changes in community structure represent responses to environmental changes that favor some species or affect interaction strength (see Chapter 8). Longer-term (e.g., successional) changes in community structure often reflect relatively predictable trends during community development on newly available or disturbed sites. Finally, changes in community structure over evolutionary time reflect responses to long-term trends in environmental conditions.

Among the major environmental issues facing governments worldwide is the effect of anthropogenic activities (e.g., altered atmospheric or aquatic chemistry, land use, species redistribution) on the composition of natural communities and the ecosystem services they provide to humans. How might changes in community structure affect epidemiology of human diseases? How stable is community structure, and how sensitive are communities and ecosystems to changes in species composition? Our perception of communities as self-organizing entities or random assemblages has significant implications for our sensitivity to species loss and our approach to management of ecosystem resources.

As with population dynamics, study of changes in community structure requires long periods of observation. Few studies have continued over sufficiently long time periods to evaluate many of the factors presumed to affect community structure. However, paleoecological evidence and studies of community recovery following disturbance have provided useful data. Research on factors affecting community structure over a range of temporal scales can enhance understanding of the degree of stability in community structure and anticipation of responses to environmental changes.

I. SHORT-TERM CHANGE IN COMMUNITY STRUCTURE

Community structure changes over relatively short time periods. Short-term variation in community structure reflects interactions among species responding differently to fluctuating abiotic conditions and species interactions. Relatively few studies measured effects of seasonal or annual changes in arthropod communities over extended periods. Several studies represent annual to decadal dynamics in arthropod communities.

Fluctuating weather conditions and disturbances can cause appreciable changes in arthropod community structure. Changes in precipitation pattern can elicit differential responses among arthropod species. Schowalter *et al.* (1999) found that particular arthropod species, as well as the entire arthropod community, associated with creosotebush, *Larrea tridentata,* in southern New Mexico showed distinct trends in abundance over an experimental gradient in precipitation volume. Abundances of several species increased with moisture availability, whereas abundances of others declined with moisture availability, and some species showed nonlinear or nonsignificant responses. Multivariate analysis indicated distinct community structures on plants subjected to different amounts of precipitation.

Polis *et al.* (1997b, 1998) studied community changes on desert islands in the Gulf of California during a 5-year period (1990–1994), which included an El Niño event (1992–1993). Winter 1992 precipitation was 5 times the historic mean and increased plant cover 10–160-fold. Insect abundance doubled in 1992 and 1993, compared to 1991 levels, with a significant shift in dominance from detritivores supported by marine litter to herbivores supported by increased plant biomass. Spider densities doubled in 1992 in response to prey abundance, but declined in 1993, despite continued high plant and prey abundance, as a result of increased abundance of parasitoid wasps, partially supported by nectar and pollen resources. These changes were consistent among islands throughout the archipelago, indicating that general processes connecting productivity and consumption governed community dynamics in this system.

Changes in precipitation pattern in western Oregon, United States, between 1986 and 1996 altered the relative abundances of dominant folivore and sapsucker species in conifer canopies (Fig. 10.1). In particular, western spruce budworm, *Choristoneura occidentalis;* sawflies, *Neodiprion abietis;* and aphids, *Cinara* spp., were abundant during a drought period, 1987–1993, but virtually absent during wetter periods. A bud moth, *Zeiraphera hesperiana,* was the dominant folivore during wet years but disappeared during the drought period.

Schowalter and Ganio (2003) described changes in arthropod community structure in tropical rainforest canopies in Puerto Rico from 1991 to 1999. Hurricane Hugo (1989) created 30–50-m diameter canopy gaps dominated by early successional shrubs, vines, and *Cecropia schreberiana* saplings. Several

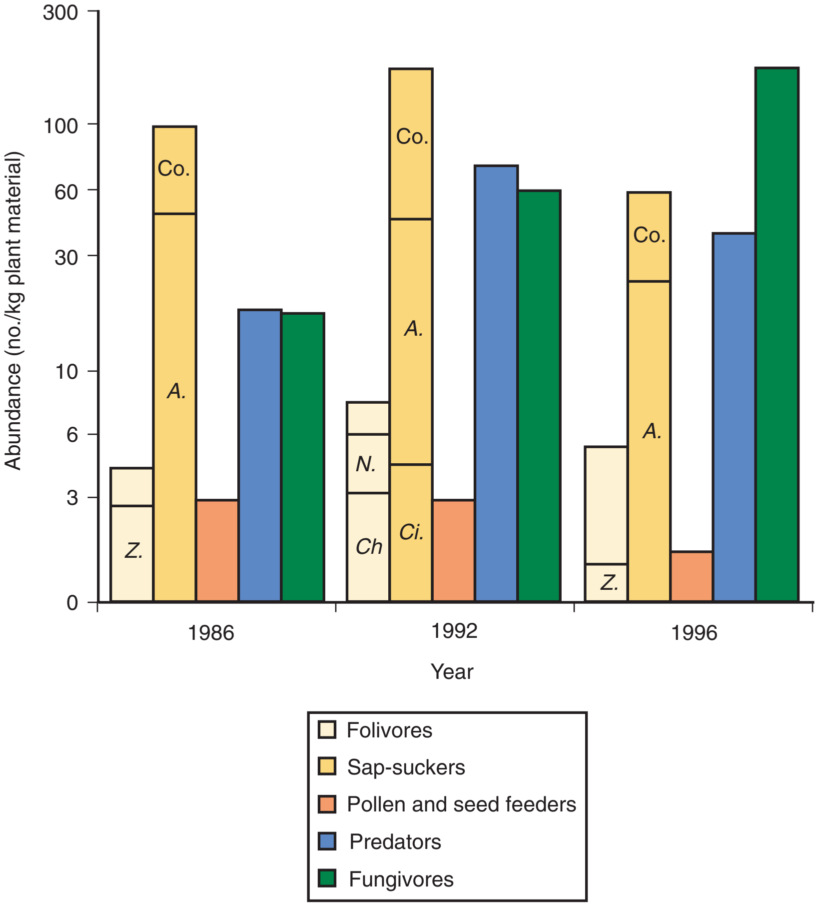


FIG. 10.1 Temporal change in arthropod abundances in old-growth Douglas fir canopies at the H. J. Andrews Experimental Forest in western Oregon; 1989 and 1996 were relatively wet years; 1992 was in the middle of an extended drought period (1987–1993). *Z., Zeiraphera hesperiana; Ch., Choristoneura occidentalis; N., Neodiprion abietis; Ci., Cinara* spp.; *A., Adelges cooleyi;* Co., Coccoidea (4 spp.). Note the log scale of abundance. Data from Schowalter (1989, 1995 and unpublished data).

species of scale insects and a phytophagous mirid bug, *Itacoris* sp., were significantly more abundant on foliage in canopy gaps, compared to nongaps, in 1991 and again following Hurricane Georges (1998), suggesting positive response to storm disturbance. Scale insect and folivore abundances were significantly more abundant during a record drought (1994–1995), compared to intervals between disturbances, providing further evidence of responses to disturbances.

Factors that increase competition or predation can reduce population sizes of particular species. Some species may become locally extinct, whereas others show population irruptions. Changes in species abundances affect interactions with other species. Both the strength and direction of interaction can change greatly. Herbivores that have little effect on their hosts at low abundances can interact in a more predatory manner at high abundances. Reduced abundance of one member of a mutualism can jeopardize the persistence of the other.

Changes in species composition and abundance alter species diversity, food web structure, and functional organization. Change in abundance of species at one trophic level can affect the diversity and abundance of species at lower trophic levels through trophic cascades. For example, reduced predator abundance usually increases herbivore abundance, thereby decreasing plant abundance (Carpenter and Kitchell 1987, 1988, Letourneau and Dyer 1998).

II. SUCCESSIONAL CHANGE IN COMMUNITY STRUCTURE

Relatively predictable changes in community structure occur over periods of decades to centuries as a result of succession on newly exposed or disturbed sites. New habitats become available for colonization as a result of tectonic activity, glacial movement, sea level change, and sediment deposition or erosion. Species colonizing newly exposed surfaces usually are small in stature, tolerant of exposure or able to exploit small shelters, and able to exploit nonorganic or exogenous resources. Disturbances to existing communities affect each species differently, depending on its particular tolerances to disturbance or postdisturbance conditions (see Chapter 2). Often, legacies from the predisturbance community (such as buried rhizomes, seed banks, woody litter, and animals surviving in protected stages or microsites) remain following disturbance and influence the trajectory of community recovery.

The process of community development on disturbed or newly exposed sites is called *ecological succession.* The succession of populations and communities on disturbed or newly exposed sites has been a unifying concept in ecology since the time of Cowles (1911) and Clements (1916). These early ecologists viewed succession as analogous to the orderly development of an organism (ontogeny). Succession progressed through a predictable sequence of stages (seres), driven by biogenic processes, which culminated in a self-perpetuating community (the climax) determined by climatic conditions. Succession is exemplified by the sequential colonization and replacement of species: weedy annual to perennial grass to forb, to shrub, to shade-intolerant tree, and finally to shade-tolerant tree stages on abandoned cropland. Succession following fire or other disturbances shows a similar sequence of stages (Fig. 10.2).

Although the succession of species and communities on newly exposed or disturbed sites is one of the best-documented phenomena in ecology, the nature of the community and mechanisms driving species replacement have been debated intensely from the beginning. Gleason (1917, 1926, 1927) argued that succession is not directed by autogenic processes but reflects population dynamics of individual species based on their adaptations to changing environmental conditions. Egler (1954) further argued that succession could proceed along many potential pathways, depending on initial conditions and initial species pools. E. Odum (1969) integrated the Clementsian model of succession with ecosystem processes by proposing that a number of ecosystem properties, including species diversity, primary productivity, biomass, and efficiency of energy and nutrient use, increase during succession. Drury and Nisbet (1973) viewed succession as a temporal gradient in community structure, similar to the spatial gradients discussed in Chapter

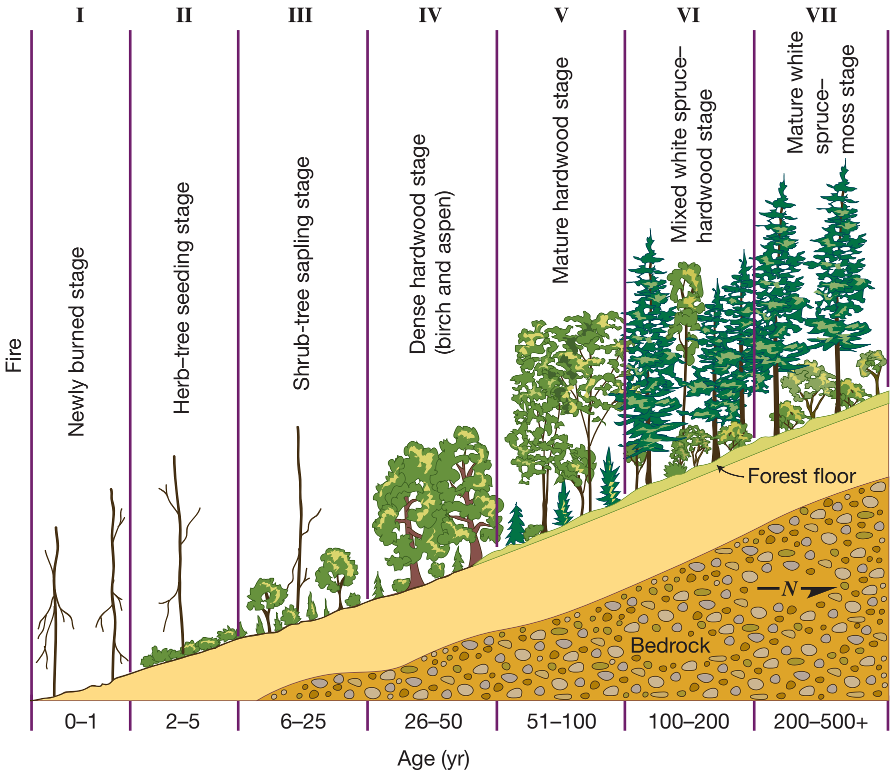


FIG. 10.2 Diagrammatic representation of upland white spruce forest succession in Alaska following fire. From van Cleve and Viereck (1981) with permission from Springer-Verlag. Please see extended permission list pg 571.

9, and argued that species physiological tolerances to environmental conditions were sufficient to explain species replacement. More recently, the importance of disturbances and heterotroph activity in determining successional processes and preventing ascension to the climatic climax has been recognized (e.g., Davidson 1993, MacMahon 1981, Ostfeld *et al.* 1997, Pickett and White 1985, Schowalter 1981, 1985, Willig and Walker 1999).

The concept of succession as goal-oriented toward a climax has succumbed to various challenges, especially recognition that succession can progress along various pathways to nonclimatic climaxes under different environmental conditions (Whittaker 1953). Furthermore, the mechanism of species replacement is not necessarily facilitation by the replaced community (e.g., Botkin 1981, Connell and Slatyer 1977, H. Horn 1981, McIntosh 1981, Peet and Christensen 1980, Whittaker 1953, 1970). Nevertheless, debate continues over the integrity of the community, the importance of autogenic factors that influence the process, and the degree of convergence toward particular community composition (Bazzaz 1990, Peet and Christensen 1980, Glenn-Lewin *et al.* 1992, West *et al.* 1981).

A. Patterns of Succession

Two types of succession can be recognized. *Primary succession* occurs on newly exposed substrates (e.g., lava flows, uplifted marine deposits, dunes, newly deposited beaches, etc.). Primary succession usually involves a long period of soil formation and colonization by species requiring little substrate modification. *Secondary succession* occurs on sites where the previous community was disturbed and is influenced by remnant substrate and surviving individuals. Although most studies of succession have dealt with trends in vegetation, heterotrophic successions, including successions dominated by insects or other arthropods, have contributed greatly to perspectives on the process. Insects and other arthropods dominate the development of freshwater communities and litter (especially woody litter and carrion) communities, and succession in these habitats occurs over shorter time scales than does succession involving longer-lived plant species.

Succession varies in duration from weeks for communities with little biomass (e.g., carrion feeders) to centuries for communities with abundant biomass (e.g., forests). Shorter successions are amenable to study by individual researchers. However, forest or desert succession spans decades to centuries and has not been studied adequately throughout its duration (see Fig. 10.2). Rather, forest succession usually has been studied by selecting plots of different age since disturbance or abandonment of management to represent various seres (i.e., the chronosequence approach). Although this approach has proved convenient for comparing and contrasting various seres, it fails to account for effects of differences in initial conditions on subsequent species colonization and turnover processes (e.g., Egler 1954, Schowalter *et al.* 1992). Even Clements (1916) noted that comparison of the successional stages is less informative than is evaluation of the factors controlling transitions between stages. However, this approach requires establishment of long-term plots protected from confounding activities and a commitment by research institutions to continue studies beyond the usual confines of individual careers. Characterization of succession is a major goal of the network of U.S. and International Long Term Ecological Research (LTER) Sites (e.g., Van Cleve and Martin 1991). Long-term and comparative studies will improve understanding of successional trajectories and their underlying mechanisms.

A number of trends have been associated with vegetation succession. Generalists or r-strategists generally dominate early successional stages, whereas specialists or K-strategists dominate later successional stages (Table 10.1, see Fig. 10.2) (Boyce 1984, V.K. Brown 1984, 1986, Brown and Hyman 1986, Brown and Southwood 1983, Grime 1977, Janzen 1977, D. Strong *et al.* 1984; see Chapter 5). Species richness usually increases during early-mid succession but reaches a plateau or declines during late succession (Peet and Christensen 1980, Whittaker 1970), a pattern similar to the spatial gradient in species richness across ecotones (Chapter 9).

E. Wilson (1969), based in part on data from Simberloff and Wilson (1969), suggested that community organization progresses through four stages: noninteractive, interactive, assortative, and evolutionary. The noninteractive stage

TABLE 10.1 Life history strategies of insects from different successional stages. Updated from V. K. Brown (1984) by permission from V. K. Brown and the American Institute of Biological Sciences, © 1984 American Institute of Biological Sciences.

Characteristic	Successional Stage				Source
	Ruderal 0–1 yr	**Early 1–5 yr**	**Mid 7–11 yr**	**Late 60+ yr**	
Mobility (% fully winged species)	94	84	80	79	Heteroptera (V. K. Brown 1982)
Generation Time (% species >1 generation/yr)	43	50	33	3	Exopterygote herbivores (V. K. Brown and Southwood 1983)
	41	37	10	12	Heteroptera (V. K. Brown 1982)
Size (mean body length, mm, ±SEM)	3.68 ± 0.57	3.59 ± 0.63	3.86 ± 0.63	4.14 ± 0.67	all insect species (V. K. Brown 1986)
Reproductive potential (mean number of embryos ±SEM)		70.0 ± 4.4*		50.2 ± 2.0 **	aphids (V. K. Brown and Llewellyn 1985)
Niche breadth (scale 1–5; 1 = highly specialized)	3.35	3.10	2.87	1.79	sap feeders (V. K. Brown and Southwood 1983)
	1.60	1.29	1.33	3.05	weevils (V. K. Brown and Hyman 1986)

* on herbaceous plants; ** on woody plants

occurs early during succession (first decade), when species richness and population densities are too low to induce density-dependent competition, predation, or parasitism. As species number increases and densities increase, interaction strength increases and produces a temporary decline or equilibrium in species number, as some species are excluded by competition or predation. The assortative stage occurs over long disturbance-free time periods as a result of species persistence in the community on the basis of efficient resource use and co-existence. Niche partitioning allows more species to colonize and persist. Finally, co-evolution over very long time periods increases the efficiency of interaction and permits further increase in species number. However, most communities are disturbed before reaching the assortative stage. The *intermediate disturbance hypothesis* predicts that species richness is maximized through intermediate levels of disturbance that maintain a combination of early and late successional species (Connell 1978, Sousa 1985).

Arthropod communities also change during vegetative succession (see Table 10.1) (V. K. Brown 1984, Shelford 1907, Weygoldt 1969). E. Evans (1988) found that grasshopper assemblages showed predictable changes following fire in a grassland in Kansas, U.S.A. The relative abundance of grass-feeding species initially increased following fire, reflecting increased grass growth, and subsequently declined, as the abundance of forbs increased.

Schowalter (1994, 1995), Schowalter and Crossley (1988), and Schowalter and Ganio (2003) reported that sap-sucking insects (primarily Homoptera) and ants dominated early successional temperate and tropical forests, whereas folivores, predators, and detritivores dominated later successional forests. This trend likely reflects the abundance of young, succulent tissues with high translocation rates that favor sap-suckers and tending ants during early regrowth.

V. K. Brown and Southwood (1983) reported a similar trend toward increased representation of predators, scavengers, and fungivores in later successional stages. They noted, in addition, that species richness of herbivorous insects and plants were highly correlated during the earliest successional stages but not later successional stages, whereas numbers of insects and host plants were highly correlated at later stages but not the earliest successional stages. Brown and Southwood (1983) suggested that early colonization by herbivorous insects depends on plant species composition but that population increases during later stages depend on the abundance of host plants (see also Chapters 6 and 7).

Punttila *et al.* (1994) reported that the diversity of ant species declined during forest succession in Finland. Most ant species were found in early successional stages, but only the three species of shade-tolerant ants were common in old (>140-year-old) forests. They noted that forest fragmentation favored species that require open habitat by reducing the number of forest patches with sufficient interior habitat for more shade-tolerant species.

Starzyk and Witkowski (1981) examined the relationship between bark- and wood-feeding insect communities and stages of oak-hornbeam forest succession. They found the highest species richness in older forest (>70 years old) with abundant dead wood and in recent clearcuts with freshly cut stumps. Densities of mining larvae also were highest in the older forest and intermediate in the recent clearcut. Intermediate stages of forest succession supported fewer species and lower densities of bark- and wood-feeding insects. These trends reflected the decomposition of woody residues remaining during early stages and the accumulation of woody debris again during later stages.

Torres (1992) reported that a sequence of Lepidoptera species reached outbreak levels on a corresponding sequence of early successional plant species during the first 6 months following Hurricane Hugo (1989) in Puerto Rico but disappeared after depleting their resources. Schowalter (unpublished data) observed this process repeated following Hurricane Georges (1998). Davidson (1993), Schowalter (1981), and Schowalter and Lowman (1999) suggested that insect outbreaks and other animal activity advance, retard, or reverse succession by affecting plant replacement by nonhost plants (see later in this chapter).

Heterotrophic successions have been studied in decomposing wood, animal carcasses, and aquatic ecosystems. These processes can be divided into distinct stages characterized by relatively discrete heterotrophic communities.

In general, succession in wood occurs over decadal time scales and is initiated by the penetration of the bark barrier by bark and ambrosia beetles (Scolytidae and Platypodidae) at, or shortly after, tree death (Ausmus 1977, Dowding 1984, Savely 1939, Swift 1977, Zhong and Schowalter 1989). These beetles inoculate galleries in fresh wood (decay class I, bark still intact) with a variety of symbiotic microorganisms (e.g., Schowalter *et al.* 1992, Stephen *et al.* 1993; see Chapter 8) and provide access to interior substrates for a diverse assemblage of saprotrophs and their predators. The bark and ambrosia beetles remain only for the first year but are instrumental in penetrating bark, separating bark from wood, and facilitating drying of subcortical tissues (initiating decay class II, bark fragmented and falling off). These insects are followed by wood-boring beetles; wood wasps; and their associated saprophytic microorganisms, which usually dominate wood for 2–10 years (Chapter 8). Powderpost and other beetles, carpenter ants, *Camponotus* spp., or termites dominate the later stages of wood decomposition (decay classes III–IV, extensive tunneling and decay in sapwood and heartwood, loss of structural integrity), which may persist for 5–100 years, depending on wood conditions (especially moisture content) and proximity to population sources. Wood becomes increasingly soft and porous, and holds more water, as decay progresses. These insects and associated bacteria and fungi complete the decomposition of wood and incorporation of recalcitrant humic materials into the forest floor (decay class V).

Insect species composition follows characteristic successional patterns in decaying carrion (Figs. 10.3 and 10.4), with distinct assemblages of species defining fresh, bloated, decay, dry, and remains stages (Payne 1965, Tantawi *et al.* 1996, Tullis and Goff 1987, Watson and Carlton 2003). For small animals, several carrion beetle species initiate the successional process by burying the carcass prior to oviposition. Distinct assemblages of insects characterize mammalian versus reptilian carcasses (Watson and Carlton 2003). For all animal carcasses, the fresh, bloated, and decay stages are dominated by various Diptera, especially calliphorids, whereas later stages are dominated by Coleoptera, especially dermestids. The duration of each stage depends on environmental conditions that affect the rate of decay (compare Figs. 10.3 and 10.4) (Tantawi *et al.* 1996)

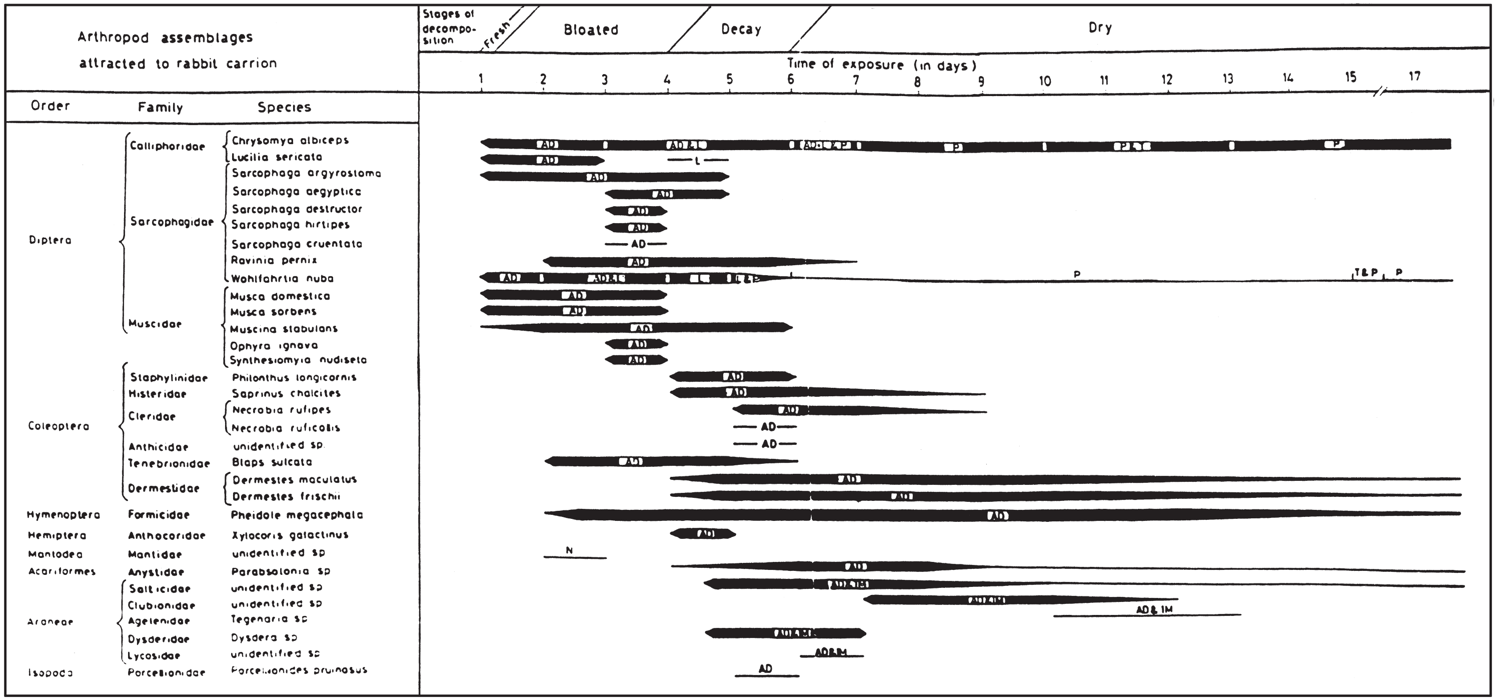


FIG. 10.3 Succession of arthropods on rabbit carrion during summer in Egypt. From Tantawi *et al.* (1996) with permission from the Entomological Society of America.

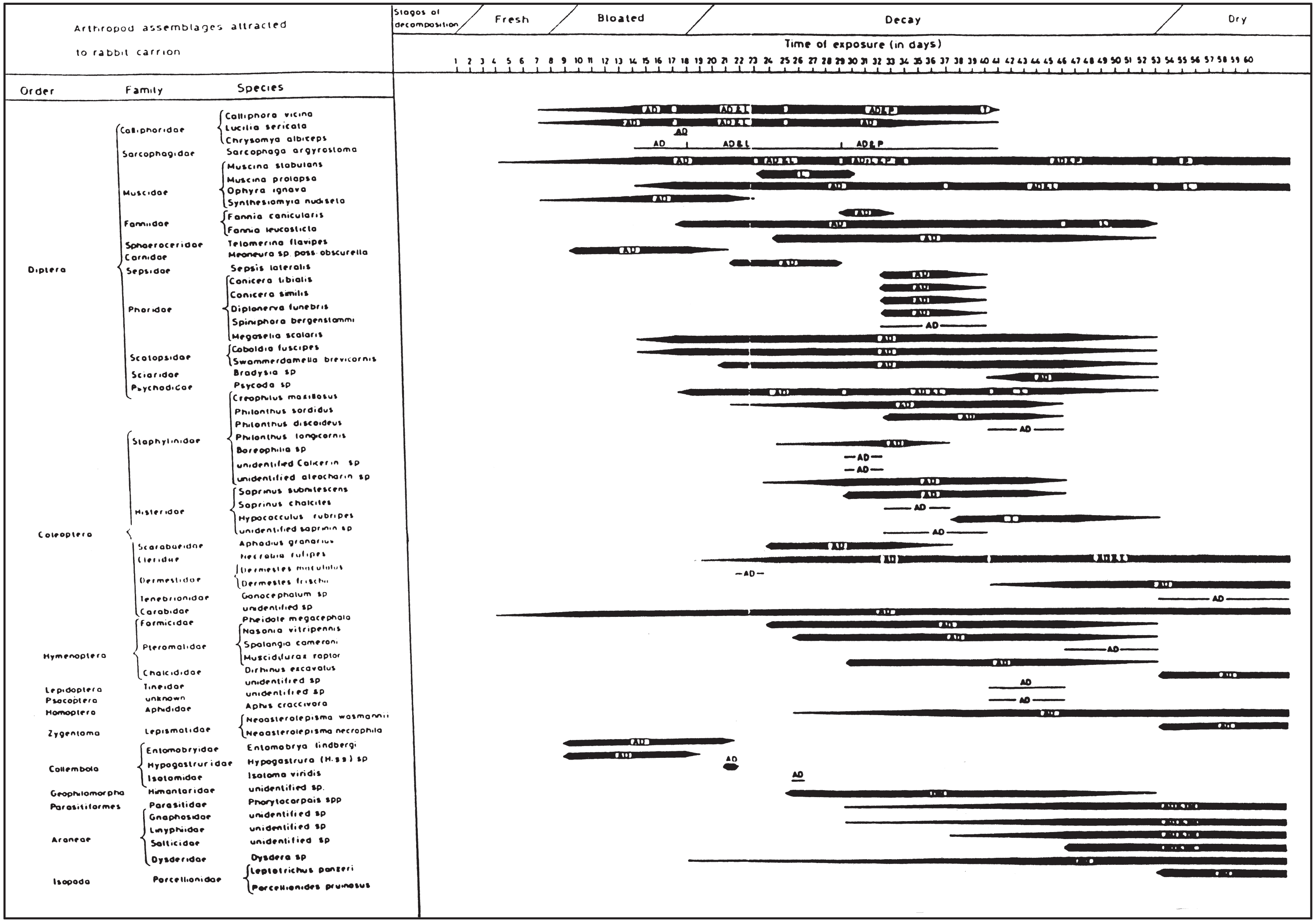


FIG. 10.4 Succession of arthropods on rabbit carrion during winter in Egypt. From Tantawi *et al.* (1996) with permission from the Entomological Society of America.

and on predators, especially ants (Tullis and Goff 1987, Wells and Greenberg 1994). This distinct sequence of insect community types, as modified by local environmental factors, has been applied by forensic entomologists to determine time since death.

Detritus-based communities develop in bromeliad and heliconia leaf pools (phytotelmata), as well as in low-order stream systems. Richardson and Hull (2000) and Richardson *et al.* (2000b) observed distinct sequences of arrival of dipteran filter feeders and gatherers during phytotelmata development in Puerto Rico. The earliest colonizer, of barely opened *Heliconia* bracts, was a small unidentified ceratopogonid, followed by an unidentified psychodid, cf. *Pericoma.* Subsequently, phytotelmata were colonized by two syrphids, *Quichuana* sp. and *Copestylum* sp. Older bracts with accumulated detritus and low oxygen concentration supported mosquitoes, *Culex antillummagnorum,* and finally tipulids, *Limonia* sp., in the oldest bracts.

B. Factors Affecting Succession

Succession generally progresses toward the community type characteristic of the biome within which it occurs (e.g., toward deciduous forest within the deciduous forest biome or toward chaparral within the chaparral biome; e.g., Whittaker 1953, 1970). However, succession can progress along various alternative pathways and reach alternative endpoints (such as stands dominated by beech, *Fagus,* maple, *Acer,* or hemlock, *Tsuga,* within the eastern deciduous forest in North America), depending on a variety of local abiotic and biotic factors. Substrate conditions represent an abiotic factor that selects a distinct subset of the regional species pool determined by climate. Distinct initial communities reflecting disturbance conditions, or unique conditions of local or regional populations, can affect the success of subsequent colonists. These initial conditions, and subsequent changes, guide succession into alternative pathways leading to distinct self-perpetuating endpoints (Egler 1954, Whittaker 1953). Herbivory and granivory can guide succession along alternative pathways (Blatt *et al.* 2001, Davidson 1993).

Substrate conditions affect the ability of organisms to settle, become established, and derive necessary resources. Some substrates restrict species representation (e.g., serpentine soils, gypsum dunes, and lava flows). Relatively few species can tolerate such unique substrate conditions or the exposure resulting from limited vegetative cover. In fact, distinct subspecies often characterize the communities on these and the surrounding substrates. Contrasting communities characterize cobbled or sandy sections of streams because of different exposure to water flow and filtration of plant or detrital resources. Finally, sites with a high water table support communities that are distinct from the surrounding communities (e.g., marsh or swamp communities embedded within grassland or forested landscapes).

Successional pathways are affected by the composition of initial colonists and survivors from the previous community. The initial colonists of a site represent regional species pools, and their composition can vary depending on proximity to population sources. A site is more likely to be colonized by abundant species than by rare species. Rapidly growing and expanding populations are more likely to colonize even marginally suitable sites than are declining populations. For example, trees dying during a period of minimal bark beetle abundance would undergo a delay in initiation of heterotrophic succession, dominated by a different assemblage of insect species associated with different microorganisms (e.g., Schowalter *et al.* 1992). Wood initially colonized by decay fungi, such as inoculated by wood-boring beetles, wasps, and termites, decays more rapidly, thereby affecting subsequent colonization, than does wood initially colonized by mold fungi, such as inoculated by bark and ambrosia beetles (Käärik 1974, Schowalter *et al.* 1992).

Many individuals survive disturbance, depending on their tolerance to (or protection from) disturbance, and affect subsequent succession (Egler 1954). Disturbance scale also affects the rate of colonization. Succession initiated primarily by ruderal colonists will differ from succession initiated by a combination of ruderal colonists and surviving individuals and propagules (e.g., seed banks). Such legacies from the previous community contribute to the early appearance and advanced development of later successional species. These may preclude establishment of some ruderal species that would lead along a different successional pathway. Large-scale disturbances promote ruderal species that can colonize a large area rapidly, whereas small-scale disturbances may expose too little area for shade-intolerant ruderal species and be colonized instead by later successional species expanding from the edge (Brokaw 1985, Denslow 1985, Shure and Phillips 1991). Fastie (1995) identified distance from each study site to the nearest seed source of Sitka spruce, *Picea sitchensis,* at the time of deglaciation as the major factor explaining among-site variance in spruce recruitment at Glacier Bay, Alaska.

The sequence of disturbances during succession determines the composition of successive species assemblages. For example, fire followed by drought would filter the community through a fire-tolerance sieve then a drought-tolerance sieve, whereas flooding followed by fire would produce a different sequence of communities. Harding *et al.* (1998) and Schowalter *et al.* (2003) demonstrated that arthropod communities in stream and forest litter, respectively, showed responses to experimental disturbances that reflected distinct community structures among blocks with different disturbance histories. Disturbance also can truncate community development. Grasslands and pine forests often dominate sites with climatic conditions that could support mesic forest, but succession is arrested by topographic or seasonal factors that increase the incidence of lightning-ignited fires and preclude persistence of mesic trees.

Longer-term environmental changes (including anthropogenic suppression of disturbances) also affect the direction of community development. Ironically, fire suppression to "protect" natural communities often results in successional replacement of fire-dominated communities, such as pine forests and grasslands. The replacing communities may be more vulnerable to different disturbances. For example, fire suppression in the intermountain region of western North America has caused a shift in community structure from relatively open, pine/larch woodland maintained by frequent ground fires to closed-canopy pine/fir forest that has become increasingly vulnerable to drought and stand replacing crown fires (Agee 1993, Schowalter and Lowman 1999, Wickman 1992).

The importance of animal activity to successional transitions has not been recognized widely, despite obvious effects of many herbivores on plant species composition (e.g., Louda *et al.* 1990a, Maloney and Rizzo 2002, Torres 1992; see Chapter 12). Vegetation changes caused by animal activity often have been attributed to plant senescence. Animals affect succession in a variety of ways (Davidson 1993, MacMahon 1981, Schowalter and Lowman 1999, Willig and McGinley 1999), and Blatt *et al.* (2001) showed that incorporation of herbivory into an old-field successional model helped to explain the multiple successional pathways that could be observed. Herbivorous species can delay colonization by host species (Tyler 1995, D. Wood and Andersen 1990) and can suppress or kill host species and facilitate their replacement by nonhosts over areas as large as 10^6 ha during outbreaks (Schowalter and Lowman 1999). Bullock (1991) reported that the scale of disturbance can affect animal activity, thereby influencing colonization and succession. Generally, herbivory and granivory during early seres halts or advances succession (V. K. Brown 1984, Schowalter 1981, Torres 1992), whereas herbivory during later seres halts or reverses succession (Davidson 1993, Schowalter and Lowman 1999). Similarly, Tullis and Goff (1987) and Wells and Greenberg (1994) reported that predaceous ants affected colonization and activity of carrion feeders and affected succession of the carrion community.

Granivores tend to feed on the largest seeds available, which most often represent later successional plant species, and thereby inhibit succession (Davidson 1993). Herbivores and granivores can interact competitively to affect local patterns of plant species survival and succession. For example, Ostfeld *et al.* (1997) reported that voles dominated interior portions of old fields, fed preferentially on hardwood seedlings over white pine, *Pinus strobes,* seedlings, and competitively displaced mice, which fed preferentially on white pine seeds over hardwood seeds near the forest edge. This interaction favored growth of hardwood seedlings in the ecotone and favored growth of white pine seedlings in the old field interior.

Animals that construct burrows or mounds or that wallow or compact soils can kill all vegetation in small (several m^2) patches or provide suitable germination habitat and other resources for ruderal plant species (D. Andersen and MacMahon 1985, MacMahon 1981; see also Chapter 14), thereby reversing succession. Several studies have demonstrated that ant and termite nests create unique habitats, usually with elevated nutrient concentrations, that support distinct vegetation when the colony is active and facilitated succession following colony abandonment (e.g., Brenner and Silva 1995, Garrettson *et al.* 1998, Guo 1998, King 1977a, b, Lesica and Kannowski 1998, Mahaney *et al.* 1999). Jonkman (1978) reported that the collapse of leaf-cutter ant, *Atta vollenweideri,* nests following colony abandonment provided small pools of water that facilitated plant colonization and accelerated development of woodlands in South American grasslands.

Predators also can affect succession. Hodkinson *et al.* (2001) observed that spiders often are the earliest colonizers of glacial moraine or other newly exposed habitats. Spider webs trap living and dead prey and other organic debris. In systems with low organic matter, nutrient availability, and microbial decomposer activity, spider digestion of prey may accelerate nutrient incorporation into the developing ecosystem. Spider webs are composed of structural proteins and may redistribute nutrients over the surface. In addition, webs physically stabilize the surface and increase surface moisture through condensation from the atmosphere. These effects of spiders may facilitate development of cyanobacterial crusts and early successional vegetation.

Relatively few studies have evaluated community development experimentally. Patterns of arthropod colonization of new habitats represent a relatively short-term succession amenable to analysis. D. Strong *et al.* (1984) considered the unwitting movement of plants around the world by humans to represent a natural experiment for testing hypotheses about development of phytophage assemblages on a new resource. They noted that relatively few arthropod colonists on exotic plants were associated with the plant in its native habitat. Most arthropods associated with exotic plants are new recruits derived from the native fauna of the new habitat. Most of the insects that colonize introduced plants are generalists that feed on a wide range of hosts, often unrelated to the introduced plant species, and most are external folivores and sap-suckers (Kogan 1981, D. Strong *et al.* 1984). Miners and gall-formers represent higher proportions of the associated fauna in the region of plant origin, likely because of the higher degree of specialization required for feeding internally. For example, endophages represented 10–30% of the phytophages associated with two species of thistles in native European communities but represented only 1–5% of phytophages associated with these thistles in southern California where they were introduced (D. Strong *et al.* 1984). These results indicate that generalists are better colonists than are specialists, but adaptation over ecological time increases exploitation efficiency (Kogan 1981, D. Strong *et al.* 1984).

In one of the most ambitious studies of community development, Simberloff and Wilson (Simberloff 1969, Simberloff and Wilson 1969, E. Wilson and Simberloff 1969) defaunated (using methyl bromide fumigation) six small mangrove islands formed by *Rhizophora mangle* in Florida Bay and monitored the reestablishment of the arthropod community during the following year. Simberloff and Wilson (1969) reported that by 250 days after defaunation, all but the most distant island had species richness and composition similar to those of untreated islands, but densities were lower on treated islands. Initial colonists included both strong and weak fliers, but weak fliers, especially psocopterans, showed the most rapid population growth. Ants, which dominated the mangrove fauna, were among the later colonists but showed the highest consistency in colonization among islands. Simberloff and Wilson (1969) found that colonization rates for ant species were related to island size and distance from population sources. The ability of an ant species to colonize increasingly smaller islands was similar to its ability to colonize increasingly distant islands. Species richness initially increased, declined gradually as densities and interactions increased, then reached a dynamic equilibrium with species colonization balancing extinction (see also E. Wilson 1969). Calculated species turnover rates were >0.67 species per day (Simberloff and Wilson 1969), consistent with the model of MacArthur and Wilson (1967).

These studies explain why early successional stages are dominated by r-selected species with wide tolerances (generalists) and rapid reproductive rates, whereas later stages are dominated by K-selected species with narrower tolerances for co-existence with more specialized species (see Chapter 5). The first arthropods to appear on newly exposed or denuded sites (also glaciated sites) usually are generalized detritivores and predators that exploit residual or exogenous dead organic material and dying colonists unable to survive. These arthropods feed on less toxic material than do herbivores or on material in which the defensive compounds have decayed. Herbivores appear only as their host plants appear, and their associated predators similarly appear as their prey appear.

C. Models of Succession

Clements (1916) noted that comparison of successional stages is less useful than is understanding of processes affecting the transitions from one sere to another. Nevertheless, few studies have continued over sufficient periods to evaluate the mechanism(s) producing successional transitions. Rather, a number of nonmutually–exclusive models, all of which may affect particular transitions to varying degrees, have been proposed and debated widely (e.g., Connell and Slatyer 1977, H. Horn 1981, McIntosh 1981, Peet and Christensen 1980). The debate involves competing views of succession as (1) resulting from population dynamics or emergent ecosystem processes and (2) as stochastic or converging on an equilibrial community structure (H. Horn 1981, McIntosh 1981).

The *facilitation model* was proposed by Clements (1916), who viewed communities as an entity that showed progressive (facilitated) development similar to the ontogeny of individual organisms. According to this model, also called *relay floristics* (Egler 1954), successive stages cause progressive changes in environmental conditions that facilitate their replacement by the subsequent stage, and later successional species cannot appear until sufficient environmental modification by earlier stages has occurred. For example, soil development or increased plant density during early stages makes the environment less suitable for recruitment of additional early, r-selected species but more suitable for recruitment of later, K-selected species. Fire-dominated ecosystems (in which nitrogen is volatilized during fire) usually are colonized following fire by symbiotic nitrogen fixers such as alders, *Alnus* spp., ceanothus, *Ceanothus* spp., or cherries, *Prunus* spp. These species are relatively shade intolerant, and increasing density eventually suppresses their photosynthesis and nitrogen fixation, facilitating replacement by shade-tolerant species growing in the understory and exploiting the replenished organic nitrogen in the soil (e.g., Boring *et al.* 1988). The increasing porosity and altered nutrient content of decomposing wood, resulting from heterotroph activity, precludes further recruitment of early successional species (e.g., bark beetles and anaerobic or microaerophilic microorganisms), and facilitates replacement by later successional wood borers and more aerobic microorganisms (e.g., Schowalter *et al.* 1992).

This model was challenged early. Gleason (1917, 1926, 1927), Whittaker (1953, 1970), and more recently Drury and Nisbet (1973) argued for a reductionist view of species colonization and turnover on the basis of individual life history attributes. Connell and Slatyer (1977), H. Horn (1981), and MacMahon (1981) proposed a broader view of succession as reflecting multiple pathways and mechanisms.

Egler (1954) argued that secondary succession often may reflect differential longevity of colonizing species. Most of the eventual dominants colonize early when competition is low. Failure of species to become established at this early stage reduces the probability of future dominance. Juveniles of later species grow to maturity over a longer period, tolerating the early dominance of ruderal species, and eventually exclude the early successional species (e.g., through shading, preemptive use of water, etc.). Connell and Slatyer (1977) referred to this model as the *tolerance model.* This model is represented best in ecosystems dominated by species that sprout from roots or stumps, germinate from seed banks, or colonize rapidly from adjacent sources. These attributes ensure early appearance along with more ruderal species. However, many large-seeded trees, flightless arthropods, and other animals characterizing later successional stages of forest ecosystems require a long period of establishment and achieve dominance only during late succession, especially in large areas of disturbed habitat (e.g., Shure and Phillips 1991).

A third model proposed by Connell and Slatyer (1977) to explain at least some successional transitions is the antithesis of facilitation. According to this *inhibition model,* the initial colonists preempt use of resources and exclude, suppress, or inhibit subsequent colonists for as long as these initial colonists persist. Succession can proceed only as individuals are damaged or killed and thereby release resources (including growing space) for other species. Examples of inhibition are successional stages dominated by allelopathic species, such as shrubs that increase soil salinity or acidity; by species that preempt space, such as many perennial sodforming grasses whose network of rhizomes restrict establishment by other plants; by species whose life spans coincide with the average interval between disturbances; and by species that create a positive feedback between disturbance and regeneration, such as eucalypts, *Eucalyptus* spp. (e.g., Shugart *et al.* 1981). In decomposing wood, the sequence of colonization by various insects determines initial fungal association; initial colonization by mold fungi can catabolize available labile carbohydrates and inhibit subsequent establishment by decay fungi (Käärik 1974), restricting further succession. Environmental fluctuation, disturbances, or animal activity (such as gopher mounds, bison wallows, trampling, and insect outbreaks) often are necessary to facilitate replacement of these stages (MacMahon 1981, Schowalter *et al.* 1981a, Schowalter and Lowman 1999). However, Agee (1993), Schowalter (1985), and Schowalter *et al.* (1981a) noted that bark beetle outbreaks increase fuel accumulation and the probability of fire, thereby ensuring the continuity of pine forest (Fig. 10.5).

H. Horn (1981) developed a model of forest succession as a tree-by-tree replacement process using the number of saplings of various species growing under each canopy species (ignoring species for which this is not a reasonable predictor of replacement) and correcting for expected longevity. This model assumes that knowing what species occupies a given position narrows the statistical range of expected future occupants and that the probability of replacement

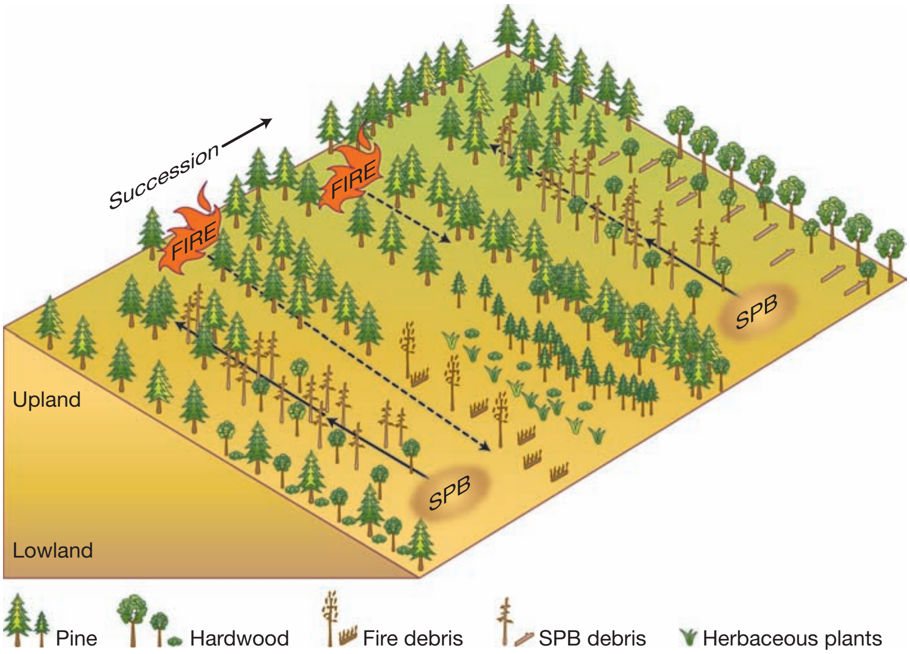


FIG. 10.5 Diagrammatic representation of interactions between southern pine beetle, *Dendroctonus frontalis,* and fire in the southeastern coniferous forest. Successional transitions extend from left to right; dotted arrows indicate direction of movement. Fire is a regular feature of the generally dry uplands but moves into generally moist lowlands where drought or southern pine beetle creates favorable conditions for combustion. Southern pine beetle is a regular feature of both forests but is most abundant where pines occur at high density and stress levels. Fire is necessary for regeneration of pines, especially following succession to hardwoods if fire return is delayed. Schowalter *et al.* (1981a) with permission from the Entomological Society of America.

depends only on the species occupying that position and does not change with time unless the occupant of that position changes. The model is not directly applicable to communities in which recurrent large-scale disturbances are the primary factor affecting vegetation dynamics. It is interesting that H. Horn (1981) found that successive iterations by a given replacement matrix invariably converged on a particular community composition, regardless of the starting composition. This result indicates that convergence is not necessarily a reflection of biotic processes (Horn 1981) and should increase attention to the rate of convergence and transition states producing convergence. E. Evans (1988) reported that grasshopper assemblage structure in replicate plots in a grassland ecosystem converged (i.e., became significantly more similar than predicted by a random model) during recovery from fire (Fig. 10.6).

Many ecologists consider vegetation changes over time to be no more than expressions of species life history characteristics. Species distributions in time reflect their physiological tolerances to changing environmental conditions,

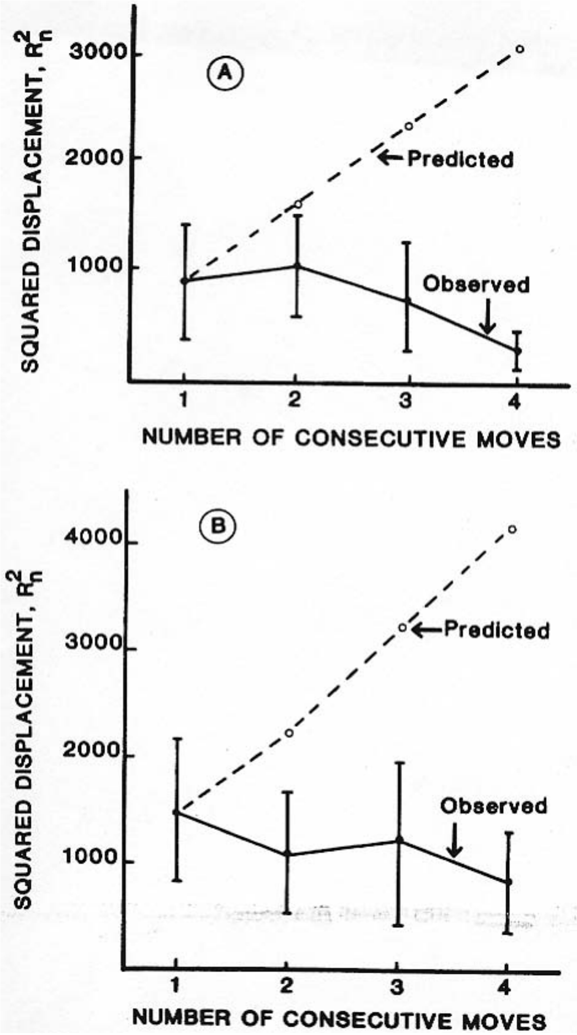


FIG. 10.6 Displacement of individual grasshopper communities (A with, and B without, the unusually common *Phoetaliotes nebrascensis*) from initial ordination positions after 1–4 "moves" (1–4 years), as observed on study sites at the Konza Prairie Long Term Ecological Research Site in Kansas, United States, 1982–1986, and as predicted by the correlated random walk model. Vertical lines represent 95% confidence limits. From E. Evans (1988) with permission from Oikos. Please see extended permission list pg 571.

parallel to distributions in space (Botkin 1981, Drury and Nisbet 1973). Several major simulation models of forest gap succession are based on species-specific growth rates and longevities as affected by stochastic mortality (e.g., Doyle 1981, Shugart *et al.* 1981, Solomon *et al.* 1981). Platt and Connell (2003) explored effects of relationships between early colonists and later colonists on species replacement following catastrophic versus noncatastrophic disturbances as explanation for variable successional trajectories, depending on disturbance severity and relative survival of early and late successional species. However, Blatt *et al.* (2001) presented the only model that currently addresses the contribution of animals to the successional process. The variety of successional pathways determined by unique combinations of interacting initial and subsequent conditions may favor models that apply chaos theory.

III. PALEOECOLOGY

Paleoecology provides a context for understanding extant interactions and community structure. Although most paleoecological study has focused on biogeographic patterns (e.g., Price 1997), fossils also reveal much about prehistoric species interactions and community structure (Labandeira 1998, Labandeira and Sepkoski 1993, Poinar and Poinar 1999) and even the consequences of prehistoric changes in climate (Wilf and Labandeira 1999, Wilf *et al.* 2001) or other disturbances (Labandeira *et al.* 2002). Similar morphological features of fossil and extant organisms imply similar functions and associated behaviors (Boucot 1990, Poinar 1993, Scott and Taylor 1983), helping to explain fossil records as well as to understand long-term patterns of community change.

The fossil record contains abundant evidence of functions and behaviors similar to those observed currently. For example, haustellate mouthparts of proto-Hemiptera suggest early appearance of feeding on plant sap (Labandeira and Sepkoski 1993, Scott and Taylor 1983). A fossil termite bug, *Termitaradus protera,* in Mexican amber has the same morphological modifications as its extant congeners for surviving in termite colonies and therefore can be assumed to have had similar interactions with termites (Poinar 1993). Dental structure of Upper Carboniferous amphibians suggests that most were predaceous and many were insectivorous (Scott and Taylor 1983).

Evidence of consistent species roles suggests that host selection behaviors and other species associations within communities have been conserved over time—the *behavioral fixity hypothesis* (Boucot 1990, Poinar 1993, Poinar and Poinar 1999). Association of potentially interacting taxa in the same deposits and anatomical evidence of interaction are common. For example, evidence of wood boring, perhaps by ancestral beetles, can be found as early as the Upper Carboniferous (Scott and Taylor 1983). Bark beetle galleries and termite nests, complete with fecal pellets, in fossil conifers from the early- to mid-Tertiary demonstrate a long evolutionary history of association between these insects and conifers (Boucot 1990, Labandeira *et al.* 2001). Some vertebrate coprolites from the Upper Carboniferous contain arthropod fragments (Scott and Taylor 1983). The presence of fig wasps (Agaonidae) in Dominican amber suggests co-occurrence of fig trees (Poinar 1993). Many fossil leaves from as early as the Upper Carboniferous show evidence of herbivory similar to that produced by modern insects (Boucot 1990, Labandeira 1998, 2002, Scott and Taylor 1983).

Boucot (1990) reported a unique example of an extant insect species associated with extant genera in an Upper Miocene deposit in Iceland. The hickory aphid, *Longistigma caryae,* occurred in the same deposit with fossil leaves of *Carya* (or *Juglans*), *Fagus, Platanus,* and *Acer.* This aphid species survives on the same tree genera in eastern North America, providing strong evidence for long-term association between this insect and its hosts.

Demonstrated interaction between pairs of species is less common but provides more convincing evidence of behavioral constancy (Fig. 10.7). Gut contents from arthropods in Upper Carboniferous coal deposits indicate herbivorous, fungivorous, or detritivorous diets for most early arthropods (Labandeira 1998, Scott and Taylor 1983). Mermithid nematodes commonly parasitize chironomid midges, usually castrating males and causing diagnostic changes in antennal morphology. A number of chironomid males from Baltic and Dominican amber show both the altered antennal morphology and the nematode emerging at the time of host death (Boucot 1990, Poinar 1993). Parasitic mites frequently are found attached to their hosts in amber. Phoretic mites associated with their beetle or fly hosts are relatively rare but occur in Dominican amber (Poinar 1993). Similarly, staphylinid beetles commensal in termite nests have been found with their termite hosts in Dominican amber (Poinar 1993).

Surprisingly few examples of demonstrated mutualistic interactions are preserved in the fossil record (Labandeira 1998, 2002). Scott and Taylor (1983) noted

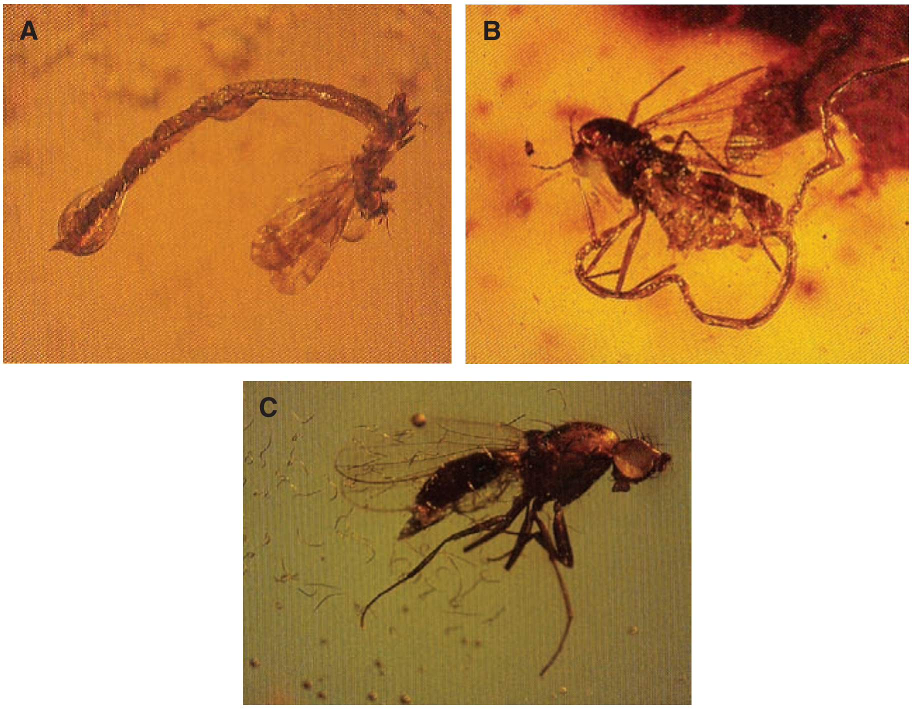


FIG. 10.7 Evidence of parasitism of extinct insects. **A:** Fungal synnema (spore-bearing structure) protruding from the body of a *Troctopsocopsis* sp. (Psocoptera) in Dominican amber. **B:** Two allantonematid nematodes emerging from a chironomid midge in Dominican amber. **C:** Parasitic nematodes radiating from a fly trapped in Dominican amber. From Poinar and Poinar (1999) with permission from Princeton University Press. Please see extended permission list pg 571.

that spores of Upper Carboniferous plants had a resistant sporoderm capable of surviving passage through animal guts, suggesting that herbivores may have served as agents of spore dispersal. An Upper Carboniferous arthropod, *Arthropleura armata,* was found with pollen grains of a medullosan seed fern attached along its posterior edge at the base of its legs. This species could have been an early pollinator of these seed ferns, whose pollen was too large for wind transport. Furthermore, some Upper Carboniferous plants produced glandular hairs that might have been an early type of nectary to attract pollinators (Scott and Taylor 1983).

Fossil data permit limited comparison of diversity and species interactions between taxonomically distinct fossil and extant communities (see also Chapter 9). Insect diversity has increased at a rate of about 1.5 families per 1 million years since the Devonian; the rise of angiosperms during the Cretaceous contributed to diversification within families but did not increase the rate of diversification at the family level (Labandeira and Sepkoski 1993). Arthropod diversity was high in the communities recorded in Upper Carboniferous coal deposits and in Dominican and Mexican ambers (Poinar 1993, Poinar and Poinar 1999, Scott and Taylor 1983). Similar associations, as discussed earlier in this section, indicate that virtually all types of interactions represented by extant communities (e.g., herbivore–plant, arthropod–fungus, predator–prey, pollinator, wood-borer, detritivore, etc.) were established as early as the Upper Carboniferous.

The behavioral fixity hypothesis permits reconstruction of prehistoric communities, to the extent that organisms associated in coal, amber, or other deposits represent prehistoric communities (e.g., Fig. 10.8) (Poinar 1993, Poinar and Poinar 1999). The Upper Carboniferous coal deposits indicate a diverse, tree fern–dominated, swamp ecosystem. The fossils in Dominican amber indicate a tropical, evergreen, angiosperm rainforest. Some insect specimens indicate the presence of large buttress-based host trees, whereas other specimens indicate the presence of palms in forest openings (Poinar 1993, Poinar and Poinar 1999). The presence of fig wasps indicates that fig trees were present. Baltic amber contains a combination of warm temperate and subtropical groups, suggesting a number of possible community structures. The temperate elements could have originated at a higher elevation, or Baltic amber may have formed during a climate change from subtropical to temperate conditions (Poinar 1993). Diversity, food web structure, and functional group organization were similar between these extinct communities and extant communities (Poinar 1993, Scott and Taylor 1983), suggesting that broad patterns of community structure are conserved through time, even as species composition changes (Poinar and Poinar 1999).

The fossil record can record changes in community structure at a site through time. The degree to which particular community types are continuous across discontinuities in the strata at a site indicates consistency of environmental conditions and community structure (Boucot 1990, Labandeira *et al.* 2002). Boucot (1990) noted that, although a particular fossilized community (taxonomic association) rarely persists long in a local stratigraphic section, communities usually recur over larger areas for 10^6–10^7 years, indicating a high degree of stability within environmental constraints. Labandeira *et al.* (2002) compiled data for insect–plant associations spanning the Cretaceous-Tertiary boundary. They found

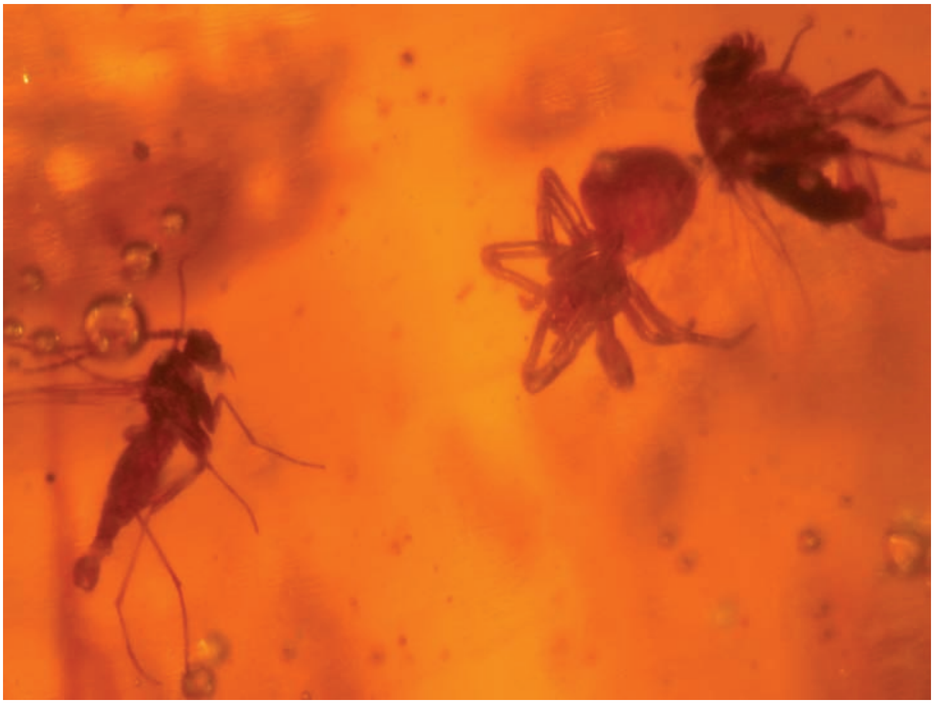


FIG. 10.8 Sciarid and phorid flies (Diptera) and spider from Columbian amber. From a sample containing >12 species of insects (4 orders) and spiders.

that specialized (monophagous) associations almost disappeared at the boundary and have not recovered to Cretaceous levels, whereas generalized (polyphagous) associations regained their Cretaceous abundances (Fig. 10.9). Wilf and Labandeira (1999) reported fossil evidence that insect herbivore diversity and intensity of herbivory increased during the global warming interval from the late Paleocene to early Eocene.

Pollen or other fossil records often indicate relatively rapid changes in distribution of particular plant species and, presumably, of associated heterotrophs. For example, Gear and Huntley (1991) reported that dating of fossilized Scots pine, *Pinus sylvestris,* stumps in northern Scotland indicated that pine forest expanded rapidly northward 70–80 km about 4000 years BP and persisted for about 400 years before retreating southward again, suggesting a 400-year period of warmer climate and community change. However, they noted that even this remarkably rapid rate of species movement would be insufficient (by an order of magnitude) to accomplish range change necessary for survival under future climate-change scenarios, especially if population spread were impeded by landscape fragmentation.

IV. DIVERSITY VERSUS STABILITY

The relationship between biodiversity and community stability remains a controversial issue (e.g., de Ruiter *et al.* 1995, Grime 1997, Hooper and Vitousek 1997, Schulze and Mooney 1993, Tilman *et al.* 1997; see Chapter 15). An early

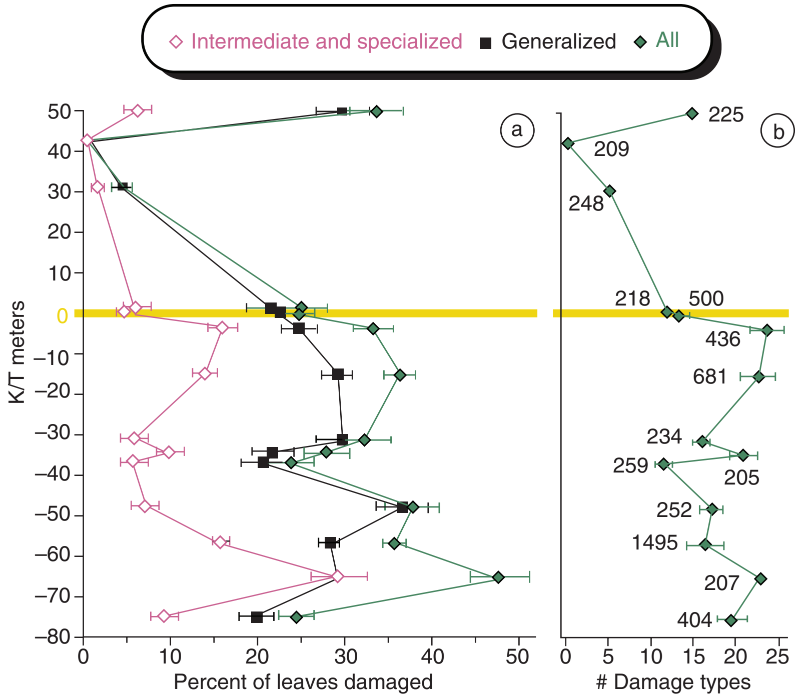


FIG. 10.9 (*a*) Frequency analyses (percentage) of insect damage for 14 stratigraphic horizons (with at least 200 specimens of identified dicot leaves) across the Cretaceous/Tertiary (K/T) boundary (orange bar) from the Williston Basin of southwestern North Dakota, United States. The horizontal scale is the percentage of leaves bearing insect damage (±1SD). The green line represents combined damage types; the black line is generalized damage types only; and the purple line is intermediate and specialized damage types. Because some individual leaves contain more than one damage type, the total percentage (green) is usually less than the sum of the two other data series. (*b*) Diversity analysis of insect damage, with raw data bootstrapped to 5,000 replicates. Vertical scale as in *a*. The data labels show the number of leaves in each sample. Poor preservation is probably responsible for the lack of recovered insect damage around the 30- to 40-m interval. From Labandeira *et al.* (2002) with permission from the National Academy of Sciences.

assumption that diversity conferred stability on communities and ecosystems was challenged, beginning in the 1970s, by modeling efforts that indicated increasing vulnerability to perturbation with system complexity (e.g., May 1973, 1981, Yodzis 1980). However, new studies have addressed the importance of biodiversity for variability of ecosystem processes (e.g., de Ruiter *et al.* 1995, Fukami *et al.* 2001, Tilman and Downing 1994, Tilman *et al.* 1997). Among these are studies of "pest" dynamics and their effects on community structure in diverse ecosystems versus simple ecosystems (e.g., Schowalter and Turchin 1993).

Fundamental to our understanding of this relationship are definitions and measurements of diversity and stability (O'Neill 2001). As noted in Chapter 9, the variety of methods for measuring diversity has complicated comparison of communities, including assessment of community change. Should diversity be measured as species richness, functional group richness, or some diversity index using species or functional groups (de Ruiter *et al.* 1995, Grime 1997, Hooper and Vitousek 1997, Tilman and Downing 1994, Tilman *et al.* 1997)? Stability can be defined as reduced variability in system behavior. However, ecologists have disagreed over how best to measure stability. Stability has been shown to have multiple components—one representing capacity to resist change, and the other representing ability to recover following a change (i.e., succession)—which indicate different degrees of stability for a given ecosystem (see the following text). The variable(s) chosen to measure stability also can indicate different degrees of stability.

Traditionally, stability was measured by population and community ecologists as the constancy of species composition and community structure (e.g., Grime 1997, May 1973, 1983). Ecosystem ecologists have emphasized the variability of ecosystem processes such as primary productivity, energy flux, and biogeochemical cycling, especially as variability changes during succession (e.g., de Ruiter *et al.* 1995, Kratz *et al.* 1995, E. Odum 1969, Tilman and Downing 1994). Species diversity may stabilize some variables but not others, or at one spatiotemporal scale but not another, leading to different conclusions. The extent to which diversity contributes to ecosystem integrity will be addressed in Chapter 15.

A. Components of Stability

Holling (1973) originally defined stability as the ability of a community to withstand disturbance with little change in structure, whereas resilience was the capacity of the community to recover following perturbation. Webster *et al.* (1975) subsequently refined the definition of stability to incorporate both *resistance* to change and *resilience* following perturbation. Succession is the expression of resilience. However, the criteria for measuring stability remain elusive. What degree of change can be accommodated before resistance is breached? Does resilience require the recovery of a predisturbance community structure or of ecosystem functions that support a particular community type, and over what scale of space or time?

Webster *et al.* (1975) developed a functional model to evaluate the relative stability of ecosystems based on the lowest turnover rates (i.e., the longest time constraint) and damping factors (i.e., factors that reduce amplitude of fluctuation) in the system. The system has not fully recovered from displacement until the slowest component of the response has disappeared. They concluded that ecosystems with greater structure and amounts of resource storage were more resistant to disturbance, whereas ecosystems with greater turnover (e.g., via consumption and succession) were more resilient. From a community standpoint, resistance depends on the level of tolerance of the dominant species to characteristic disturbances or other environmental changes (e.g., through protected meristems or propagules) or resource storage; resilience is conferred by species with rapid recolonization and growth rates. Overall, temperate forests, with high biotic and abiotic storage and slow turnover, appear to be most resistant but least resilient to disturbance, and stream systems, with low biotic and abiotic storage and high turnover, appear to be least resistant but most resilient. Resistance and resilience were found to be related inversely, with their relative contributions to stability in a given ecosystem determined by the proportions of K and r specialists (see Chapter 15). Succession appears to represent a trend from more resilient to more resistant communities.

Resistance and resilience are affected by regional species abundance and distribution. Resistance can be compromised by fragmentation, which increases community exposure to external factors. For example, trees in interior forest communities usually are buffered from high temperatures and high wind speeds by surrounding trees and usually have less buttressing than open-grown trees. Fragmentation increases the proportion of trees exposed to high temperatures and wind speeds and thereby vulnerable to moisture stress or toppling (J. Chen *et al.* 1995, Franklin *et al.* 1992). Fragmentation also interferes with the adapted abilities of species in the regional pool to recolonize disturbed sites. Species are adapted to levels of dispersal and colonization sufficient to maintain populations within the characteristic habitat matrix of the landscape. If the rate of patch turnover is increased through fragmentation, the colonization rates for many species may be insufficient to provide the necessary level of resilience for community recovery. Such changes in landscape condition may bias evaluation of community stability.

B. Stability of Community Variables

A number of community variables can be examined from the standpoint of their variability with respect to diversity. Among these are species composition and food web structure. Simpler communities, in terms of species composition and food web structure, often appear to be more stable than complex communities (e.g., May 1973, 1983). Boucot (1990) noted that simple marine communities in the fossil record continue across sedimentary discontinuities more often than do complex marine communities. Boucot (1990) also noted that particular taxonomic associations usually recur over larger areas for 10^6–10^7 years, indicating a high degree of stability within environmental constraints. The variety of successional pathways leading to multiple endpoints (H. Horn 1981, Whittaker 1953) also has indicated that many communities do not necessarily recover their predisturbance composition or food web structure, although some mechanisms lead to positive feedback between disturbance and community organization (Schowalter 1985, Schowalter *et al.* 1981a, Shugart *et al.* 1981).

Modeling approaches have led to contrasting conclusions. May (1973, 1983) and Yodzis (1980) reported that more complex communities were more vulnerable to disruption by perturbations in any particular species population because of their propagation through the network of interactions involving that species. However, de Ruiter *et al.* (1995) incorporated the patterning of interaction strengths in real communities and found that simultaneous occurrence of strong top-down regulation of lower trophic levels and strong bottom-up regulation of higher trophic levels imposed stabilizing patterns on interaction strengths. E. Evans (1988) found that grasshopper assemblages converged toward significantly greater similarity in structure following fire in a grassland ecosystem than predicted by a random model. Fukami *et al.* (2001) modeled compartmentalized communities and demonstrated that increasing biodiversity increased similarity in composition among local communities and that greater similarity improved reliability of community structure and function.

Diversity may dampen the spread of insects or pathogens that could threaten some species, hence disrupting community structure. For example, the diversity of pines and hardwoods in the southern United States reduces spread of southern pine beetle populations (Schowalter and Turchin 1993). Ostfeld and Keesing (2000) found that the number of human cases of Lyme disease, caused by the tick-vectored spirochete, *Borrelia burgdorferi*, declined with species richness of small mammals and lizards but increased with species richness of ground-dwelling birds (Fig. 10.10). These data indicated that disease epidemiology may depend on the diversity of reservoir hosts, but disease incidence generally should decline with increasing dilution of reservoir hosts by nonhosts.

To some extent, lack of a clear correlation between diversity and stability of community variables may be an artifact of the duration of succession or the number of intermediate stages that can generate alternative pathways. More frequently disturbed communities may appear to be more stable than infrequently disturbed communities because the ecological attributes of ruderal species favor rapid recovery, whereas longer time periods and more intervening factors affect recovery of tree species composition. Furthermore, if maximum species diversity occurs at intermediate levels of disturbance (the *intermediate disturbance hypothesis*), then the lower species diversity of earlier and later successional communities is associated with both high and low stability in terms of frequency and amplitude of departure from particular community structure.

A major source of diversity is the variety of community types and the regional species pool maintained in a shifting landscape mosaic of patch types. Although the community of any particular site may appear unstable because of multiple factors interacting to affect its response to perturbation, the landscape pattern of local communities minimizes the distance between population sources and sinks and ensures proximity of colonists for species packing and assortment during site recovery. Even if the community does not recover to the same endpoint, that predisturbance endpoint likely appears in other patches.

Furthermore, diverse, or complex, communities can be compartmentalized spatially as a result of heterogeneity of resources and population growth patterns (see Chapters 7 and 9). As Boucot (1990) noted, fossil communities rarely persist long at a site but recur over larger areas for long time periods, indicating a high degree of stability at a landscape scale. Hence, species composition and community structure may be conditionally stable at the landscape scale but not at the site scale, with the landscape-scale community represented as a shifting mosaic of local component communities.

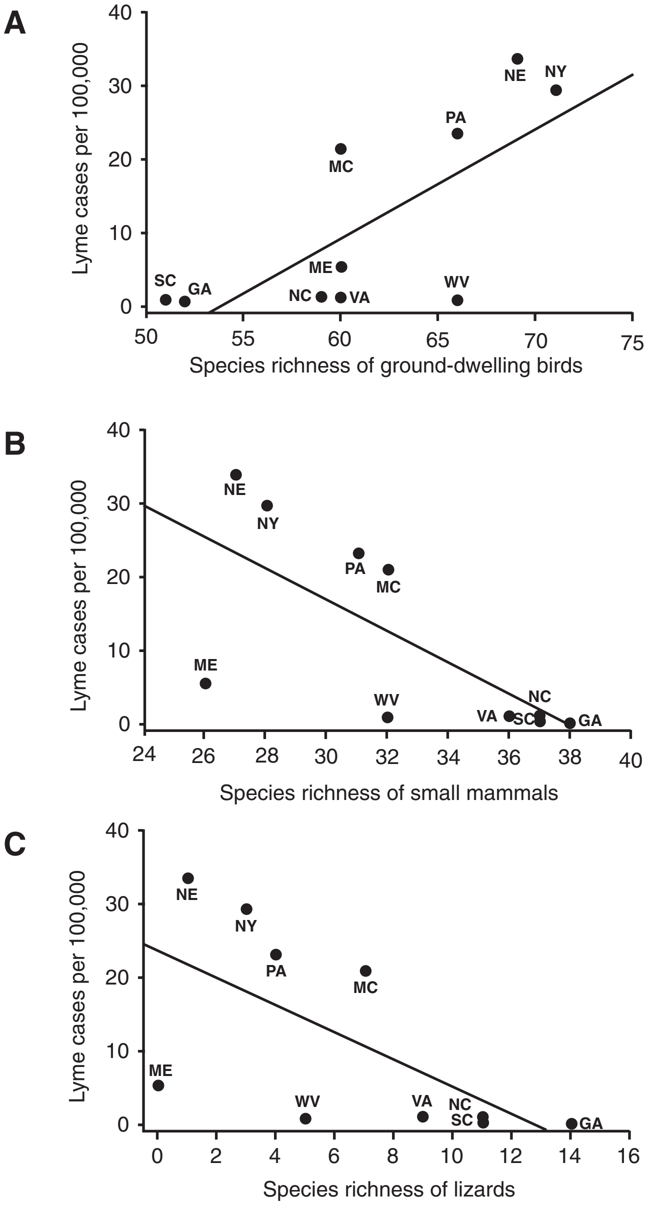


FIG. 10.10 Relationship between reported cases of human Lyme disease in 1996 and species richness of ground-dwelling birds (*A*), small mammals (*B*), and lizards (*C*) in the eastern United States. GA, Georgia; MC, Mid-Atlantic states; ME, Maine; NC, North Carolina; NE, New England states; NY, New York; PA, Pennsylvania; SC, South Carolina; VA, Virginia; and WV, West Virginia. From Ostfeld and Keesing (2000) with permission from Conservation Biology. Please see extended permission list pg 571.

V. SUMMARY

Community structure changes over a range of time scales, from annual to decadal to millenial time periods. Temporal patterns of community organization and their sensitivity to environmental changes can indicate their stability to anthropogenic changes.

Community structure changes on annual time scales as population sizes respond to environmental conditions. Changes in resource quality, competition, and predation lead to population irruptions of some species and local extinction of others, thereby affecting their interactions with other species and leading to changes in community structure.

Ecological succession, the sequential stages of community development on newly exposed or disturbed sites, is one of the best documented ecological phenomena and has provided a unifying concept that integrates species life history strategies, population behavior, community dynamics, and ecosystem processes. Early successional communities usually are dominated by relatively generalized ruderal species with high mobility and rapid reproductive rates. Later successional stages are increasingly dominated by species that are more specialized, are less mobile, and have lower reproductive capacities. Although most studies of succession have focused on plants, insects show successional patterns associated with changes in vegetation, and the relatively rapid heterotrophic succession in decomposing wood and animal carcasses has contributed much to successional theory.

A number of factors influence successional pathways. Local substrate conditions can restrict initial colonists to those from the surrounding species pool that can become established on distinct substrates, such as serpentine, volcanic, or water-saturated soils. The composition of the initial community, including survivors of the previous disturbance and colonists, can affect the success of subsequent colonists. Subsequent disturbances and animal activity can affect successional pathways. Animals, including insects, create germination sites for colonists and suppress some host species, thereby facilitating, inhibiting, or reversing succession. In fact, animal activity often may account for vegetation changes that have been attributed to plant senescence.

Several models of succession have augmented the early model of succession as a process of facilitated community development, in which earlier stages create conditions more conducive to successive stages. In some cases, all the eventual dominants are present in the initial community, and succession reflects differential development time and longevity among species (i.e., the tolerance model). Some successional stages are able to competitively exclude later colonists, the inhibition model. Succession may advance beyond such stages as a result of plant injury or death from subsequent disturbances or animal activity.

Paleoecological research indicates that species interactions and community structures have been relatively consistent over evolutionary time. However, the communities occupying particular sites have changed over these time periods as the environmental conditions of the site have changed.

The relationship between species or functional diversity and community or ecosystem stability has been highly controversial. Much of the discussion reflects different definitions of diversity and stability. Stability can be seen to have two major components: resistance to change and resilience following perturbation. Succession is the expression of resilience. Although much evidence indicates that a particular community composition or structure may not be replaced at a site, indicating instability at the local level, the structure of communities at a landscape scale ensures that disturbed sites are near population sources and that component communities are maintained within a shifting landscape mosaic, indicating stability at the landscape or regional level.

SECTION IV

ECOSYSTEM LEVEL

THE ECOSYSTEM LEVEL OF ORGANIZATION INTEGRATES species interactions and community structure with their responses to, and effects on, the abiotic environment. Interactions among organisms are the mechanisms governing energy and nutrient fluxes through ecosystems. The rates and spatial patterns in which individual organisms and populations acquire and allocate energy and nutrients determine the rate and direction of these fluxes (see Chapters 4 and 8).

Communities vary in their ability to modify their abiotic environment. The relative abundance of various nutrient resources affects the efficiency with which they are cycled and retained within the ecosystem. Increasing biomass confers increased storage capacity and buffering against changes in resource availability. Community structure also can modify climatic conditions by controlling albedo and hydric fluxes, buffering individuals against changing environmental conditions.

A major issue at the ecosystem level is the extent to which communities are organized to maintain optimal conditions for the persistence of the community. Species interactions and community structures may represent adaptive attributes at the supraorganismal level that stabilize ecosystem properties near optimal levels for the various species. If so, anthropogenic interference with community organization (e.g., species redistribution, pest control, overgrazing, deforestation) may disrupt stabilizing mechanisms and contribute to ecosystem degradation.

Insects affect virtually all ecosystem properties, especially through their effects on vegetation, detritus, and soils. Insects clearly affect primary productivity, hence the capture and flux of energy and nutrients. In fact, insects are the dominant pathway for energy and nutrient flow in many aquatic and terrestrial ecosystems.

They affect vegetation density and porosity, hence albedo and the penetration of light, wind, and precipitation. They affect accumulation and decomposition of litter and mixing and porosity of soil and litter, thereby affecting soil fertility and water flux. They often determine disturbance frequency, succession, and associated changes in efficiency of ecosystem processes over time. Their small size and rapid and dramatic responses to environmental changes are ideal attributes for regulators of ecosystem processes, through positive and negative feedback mechanisms. Ironically, effects of detritivores (largely ignored by insect ecologists) on decomposition have been addressed by ecosystem ecologists, whereas effects of herbivorous insects (the focus of insect ecologists) on ecosystem processes have been all but ignored by ecosystem ecologists until recently.

Chapter 11 summarizes key aspects of ecosystem structure and function, including energy flow, biogeochemical cycling, and climate modification. Chapters 12–14 cover the variety of ways in which insects affect ecosystem structure and function. The varied effects of herbivores are addressed in Chapter 12. Although not often viewed from an ecosystem perspective, pollination and seed predation affect patterns of plant recruitment and primary production as described in Chapter 13. The important effects of detritivores on organic matter turnover and soil development are the focus of Chapter 14. Finally, the potential roles of these organisms as regulators of ecosystem processes are explored in Chapter 15.

11

Ecosystem Structure and Function

TANSLEY (1935) COINED THE TERM "ECOSYSTEM" TO RECOGNIZE THE integration of the biotic community and its physical environment as a fundamental unit of ecology within a hierarchy of physical systems that span the range from atom to universe. Shortly thereafter, Lindeman's (1942) study of energy flow through an aquatic ecosystem introduced the modern concept of an ecosystem as a feedback system capable of redirecting and reallocating energy and matter fluxes. More recently, during the 1950s through the 1970s, concern over the fate of radioactive isotopes from nuclear fallout generated considerable research on biological control of elemental movement through ecosystems (Golley 1993). Recognition of anthropogenic effects on atmospheric conditions, especially greenhouse gas and pollutant concentrations, has renewed interest in how natural and altered communities control fluxes of energy and matter and modify abiotic conditions.

Delineation of ecosystem boundaries can be problematic. Ecosystems can be described at various scales. At one extreme, the diverse flora and fauna living on the backs of rainforest beetles (Gressitt *et al.* 1965, 1968) or the aquatic communities in water-holding plant structures (Richardson *et al.* 2000a, b) (Fig. 11.1) constitute an ecosystem. At the other extreme, the interconnected terrestrial and marine ecosystems constitute a global ecosystem (Golley 1993, J. Lovelock 1988, Tansley 1935). Generally, ecosystems have been described at the level of the

Fig. 11.1 The community of aquatic organisms, including microflora and invertebrates, that develops in water-holding structures of plants, such as *Heliconia* flowers, represents a small-scale ecosystem with measurable inputs of energy and matter, species interactions that determine fluxes and cycling of energy and matter, and outputs of energy and matter.

landscape patch composed of a relatively distinct community type. However, increasing attention has been given to the interconnections among patches that compose a broader landscape-level or watershed-level ecosystem (e.g., O'Neill 2001, Polis *et al.* 1997a, Vannote *et al.* 1980).

Ecosystems can be characterized by their structure and function. Structure reflects the way in which the ecosystem is organized (e.g., species composition, distribution of energy, and matter [biomass], and trophic or functional organization in space). Function reflects the biological modification of abiotic conditions, including energy flow, biogeochemical cycling, and soil and climate modification. This chapter describes the major structural and functional parameters of ecosystems to provide the basis for description of insect effects on these parameters in Chapters 12–14. Insects affect ecosystem structure and function in a number of ways and are primary pathways for energy and nutrient fluxes.

I. ECOSYSTEM STRUCTURE

Ecosystem structure represents the various pools (both sources and sinks) of energy and matter and their relationships to each other (i.e., directions of matter or information flow; e.g., Fig. 1.3). The size of these pools (i.e., storage capacity) determines the buffering capacity of the system. Ecosystems can be compared on the basis of the sizes and relationships of various biotic and abiotic compartments for storage of energy and matter. Major characteristics for comparing ecosystems are their trophic or functional group structure, biomass distribution, or spatial and temporal variability in structure.

A. Trophic Structure

Trophic structure represents the various feeding levels in the community. Organisms generally can be classified as *autotrophs* (or primary producers), which synthesize organic compounds from abiotic materials, and *heterotrophs* (or secondary producers), including insects, which ultimately derive their energy and resources from autotrophs (Fig. 11.2).

Autotrophs are those organisms capable of fixing (acquiring and storing) inorganic resources in organic molecules. Photosynthetic plants, responsible for fixation of abiotic carbon into carbohydrates, are the sources of organic molecules. This chemical synthesis is powered by solar energy. Free-living and symbiotic N-fixing bacteria and cyanobacteria are an important means of converting inorganic N_2 into ammonia, the source of most nitrogen available to plants. Other chemoautotrophic bacteria oxidize ammonia into nitrite or nitrate (the form of nitrogen available to most green plants) or oxidize inorganic sulfur into organic compounds. Production of autotrophic tissues must be sufficient to compensate for amounts consumed by heterotrophs.

Heterotrophs can be divided into several trophic levels depending on their source of food. Primary consumers (herbivores) eat plant tissues. Secondary consumers eat primary consumers, tertiary consumers eat secondary consumers, and so on. Omnivores feed on more than one trophic level. Finally, reducers

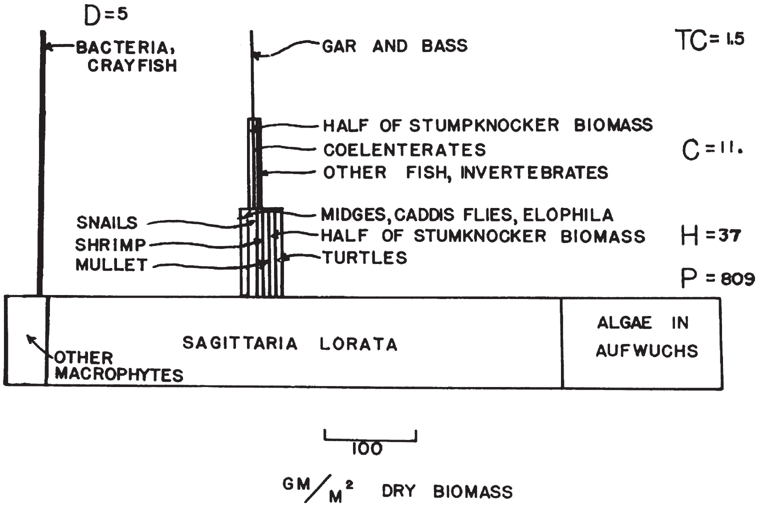


Fig. 11.2 Biomass pyramid for the Silver Springs ecosystem. P, primary producers; H, herbivores; C, predators; TC, top predators; D, decomposers. From H. Odum (1957) with permission from the Ecological Society of America.

(including detritivores and decomposers) feed on dead plant and animal matter (Whittaker 1970). Detritivores fragment organic material and facilitate colonization by decomposers, which catabolize the organic compounds.

Each trophic level can be subdivided into functional groups, based on the way in which organisms gain or use resources (see Chapter 9). For example, autotrophs can be subdivided into photosynthetic, nitrogen-fixing, nitrifying, and other functional groups. The photosynthetic functional group can be subdivided further into ruderal, competitive, and stress-tolerant functional groups (e.g., Grime 1977) or into C-3 and C-4, nitrogen-accumulating, calcium-accumulating, high-lignin or low-lignin functional groups, etc., to represent their different strategies for resource use and growth. Similarly, primary consumers can be subdivided into migratory grazers (e.g., many ungulates and grasshoppers), sedentary grazers (various leaf-chewing insects), leaf miners, gall-formers, sap-suckers, root feeders, parasitic plants, plant pathogens, etc., to reflect different modes for acquiring and affecting their plant resources.

The distribution of biomass in an ecosystem is an important indicator of storage capacity, a characteristic that influences ecosystem stability (Webster *et al.* 1975; Chapter 15). Harsh ecosystems, such as tundra and desert, restrict autotrophs to a few small plants with relatively little biomass to store energy and matter. Dominant species are adapted to retain water, but water storage capacity is limited. By contrast, wetter ecosystems permit development of large producers with greater storage capacity in branch and root systems. Accumulated detritus represents an additional pool of stored organic matter that buffers the ecosystem from changes in resource availability. Tropical and other warm, humid ecosystems generally have relatively low detrital biomass because of rapid decomposition and turnover. Stream and tidal ecosystems lose detrital material as a result of export in flowing water. Detritus is most likely to accumulate in cool, moist ecosystems, especially boreal forest and deep lakes, in which detritus decomposes slowly. Biomass of heterotrophs is relatively small in most terrestrial ecosystems, but it may be larger than primary producer biomass in some aquatic ecosystems, as a result of high production and turnover by small biomass of algae (Whittaker 1970).

Trophic structure can be represented by numbers, mass (biomass), or energy content of organisms in each trophic level (see Fig. 11.2). Such representations are called numbers pyramids, biomass pyramids, or energy pyramids (see Elton 1939) because the numbers, mass, and energy content of organisms generally decline at successively higher trophic levels. However, the form of these pyramids differs among ecosystems. Terrestrial ecosystems usually have large numbers or biomasses of primary producers that support progressively smaller numbers or biomasses of consumers. Many stream ecosystems are supported primarily by allochthonous material (detritus or prey entering from the adjacent terrestrial ecosystem) and have few primary producers (e.g., Cloe and Garman 1996, Oertli 1993, J. Wallace *et al.* 1997, Wipfli 1997). Numbers pyramids for terrestrial ecosystems may be inverted because individual plants can support numerous invertebrate consumers. Biomass pyramids for some aquatic ecosystems are inverted because a small biomass of plankton with a high rate of reproduction and turnover can support a larger biomass of organisms with low rates of turnover at higher trophic levels (Whittaker 1970).

B. Spatial Variability

At one time, the ecosystem was considered to be the interacting community and abiotic conditions of a site. This view gradually has expanded to incorporate the spatial pattern of interacting component communities at a landscape or watershed level (see Chapter 9). Patches within a landscape or watershed are integrated by disturbance dynamics and interact through the movement of organisms, energy, and matter (see Chapter 7). For example, the stream continuum concept (Vannote *et al.* 1980) integrates the various stream sections that mutually influence each other. Downstream ecosystems are influenced by inputs from upstream, but the upstream ecosystems are influenced by organisms returning materials from downstream (e.g., Pringle 1997). Soils represent substantial storage of carbon and nutrients in some patches but may contain little carbon and nutrients in adjacent patches connected by water flux. Riparian zones (floodplains) connect terrestrial and aquatic ecosystems. Periodic flooding and emerging arthropods move sediments and nutrients from the aquatic system to the terrestrial system; runoff and falling litter and terrestrial arthropods move sediments and nutrients from the terrestrial to the aquatic system (Cloe and Garman 1996, Wipfli 1997). The structure of riparian and upslope vegetation influence the interception and flow of precipitation (rain and snow) into streams (Post and Jones 2001). The structure of ecosystems at a stream continuum or landscape scale may have important consequences for recovery from disturbances by affecting proximity of population sources and sinks. Patches representing various stages of recovery from disturbance provide the sources of energy and matter (including colonists) for succession in disturbed patches. Important members of some trophic levels, especially migratory herbivores, birds, and anadromous fish, often are concentrated seasonally at particular locations along migratory routes. Social insects may forage long distances from their colonies, integrating patches through pollination, seed dispersal, or other interactions. Such aggregations add spatial complexity to trophic structure.

II. ENERGY FLOW

Life represents a balance between the tendency to increase entropy (Second Law of Thermodynamics) and the decreased entropy through continuous energy inputs necessary to concentrate resources for growth and reproduction. All energy for life on Earth ultimately comes from solar radiation, which powers the chemical storage of energy through photosynthesis. Given the First and Second Laws of Thermodynamics, the energy flowing through ecosystems, including resources harvested for human use, can be no greater, and usually is much less, than the amount of energy stored in carbohydrates.

Organisms have been compared to thermodynamic machines powered by the energy of carbohydrates to generate maximum power output in terms of work and progeny (Lotka 1925, H. Odum and Pinkerton 1955, Wiegert 1968). Just as organisms can be studied in terms of their energy acquisition, allocation, and energetic efficiency (Chapter 4), so ecosystems can be studied in terms of their energy acquisition, allocation, and energetic efficiency (E. Odum 1969, H. Odum and Pinkerton 1955). Energy acquired from the sun powers the chemical synthesis of carbohydrates, which represents storage of potential energy that is then channeled through various trophic pathways, each with its own power output, and eventually is dissipated completely as heat through the combined respiration of the community (Lindeman 1942, E. Odum 1969, H. Odum and Pinkerton 1955).

The study of ecosystem energetics was pioneered by Lindeman (1942), whose model of energy flow in a lacustrine ecosystem ushered in the modern concept of the ecosystem as a thermodynamic machine. Lindeman noted that the distinction between the community of living organisms and the nonliving environment is obscured by the gradual death of living organisms and conversion of their tissues into abiotic nutrients that are reincorporated into living tissues.

The rate at which available energy is transformed into organic matter is called productivity. This energy transformation at each trophic level (as well as by each organism) represents the storage of potential energy that fuels metabolic processes and power output at each trophic level. Energy flow reflects the transfer of energy for productivity by all trophic levels.

A. Primary Productivity

Primary productivity is the rate of conversion of solar energy into plant matter. The total rate of solar energy conversion into carbohydrates (total photosynthesis) is *gross primary productivity* (GPP). However, a portion of GPP must be expended by the plant through metabolic processes necessary for maintenance, growth, and reproduction and is lost as heat through respiration. The net rate at which energy is stored as plant matter is *net primary productivity.* The energy stored in net primary production (NPP) becomes available to heterotrophs.

Primary productivity, turnover, and standing crop biomass are governed by a number of factors that differ among successional stages and between terrestrial and aquatic ecosystems. NPP is correlated with foliar standing crop biomass (Fig. 11.3). Hence, reduction of foliar standing crop biomass by herbivores can affect NPP. Often, only above-ground NPP is measured, although below-ground production usually exceeds above-ground production in grassland and desert ecosystems (W. Webb *et al.* 1983). Among major terrestrial biomes, total (above-ground + below-ground) NPP ranges from 2000 g m^{-2} $year^{-1}$ in tropical forests, swamps and marshes, and estuaries to <200 g m^{-2} $year^{-1}$ in tundra and deserts (Fig. 11.4) (S. Brown and Lugo 1982, Waide *et al.* 1999, W. Webb *et al.* 1983, Whittaker 1970).

Photosynthetic rates and NPP are sensitive to environmental conditions. Photosynthetic rate and NPP increase with precipitation up to a point, after which they decline as a result of low light associated with cloudiness and reduced nutrient availability associated with saturated soils (Schuur *et al.* 2001). These

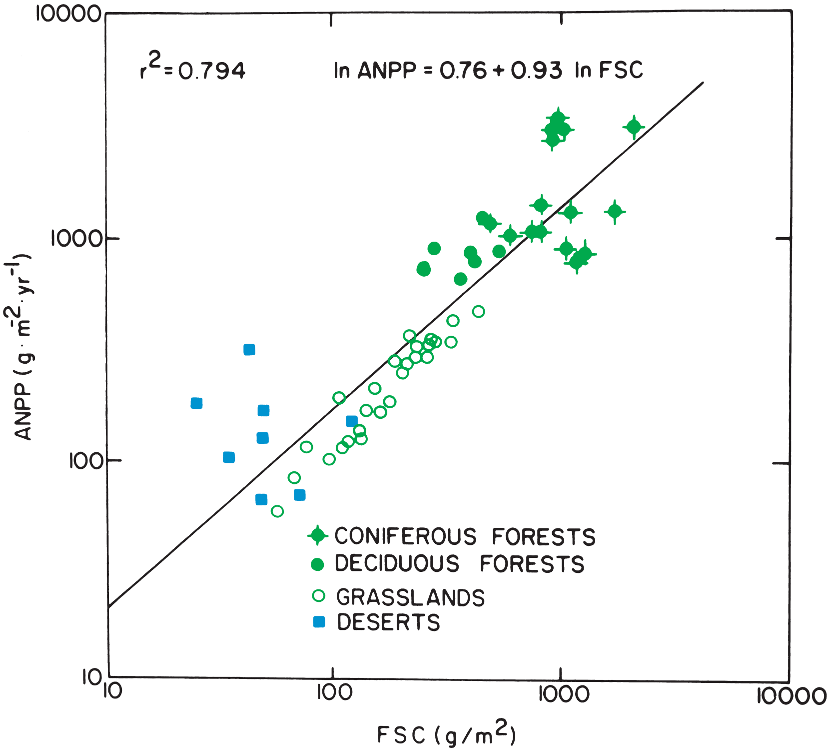


Fig. 11.3 Relationship between above-ground net primary production (ANPP) and peak foliar standing crop (FSC) for forest, grassland, and desert ecosystems. From W. Webb *et al.* (1983) with permission from the Ecological Society of America.

rates also increase with temperature, up to a point at which water loss causes stomatal closure (Whittaker 1970).

Photosynthetically active radiation occurs within the range of 400–700 nm. The energy content of NPP divided by the supply of short-wave radiation, on an annual basis, provides a measure of photosynthetic efficiency (W. Webb *et al.* 1983). Photosynthetic efficiency generally is low, ranging from 0.065% to 1.4% for ecosystems with low to high productivities, respectively (Sims and Singh 1978, Whittaker 1970).

Photosynthetically active radiation can be limited as a result of latitude, topography, cloud cover, or dense vegetation, which restrict penetration of short-wave radiation. Terborgh (1985) discussed the significance of differences in tree geometries among forest biomes. Boreal tree crowns are tall and narrow to maximize interception of lateral exposure to sunlight filtered through a greater thickness of atmosphere, whereas tropical tree crowns are umbrella shaped to maximize interception of sunlight filtered through the thinner layer of atmosphere overhead. Solar penetration through tropical tree canopies, but not boreal tree canopies, is sufficient for development of multiple layers of understory plants.

The relationship between precipitation and potential evapotranspiration (PET) is an important factor affecting photosynthesis. Water limitation can result

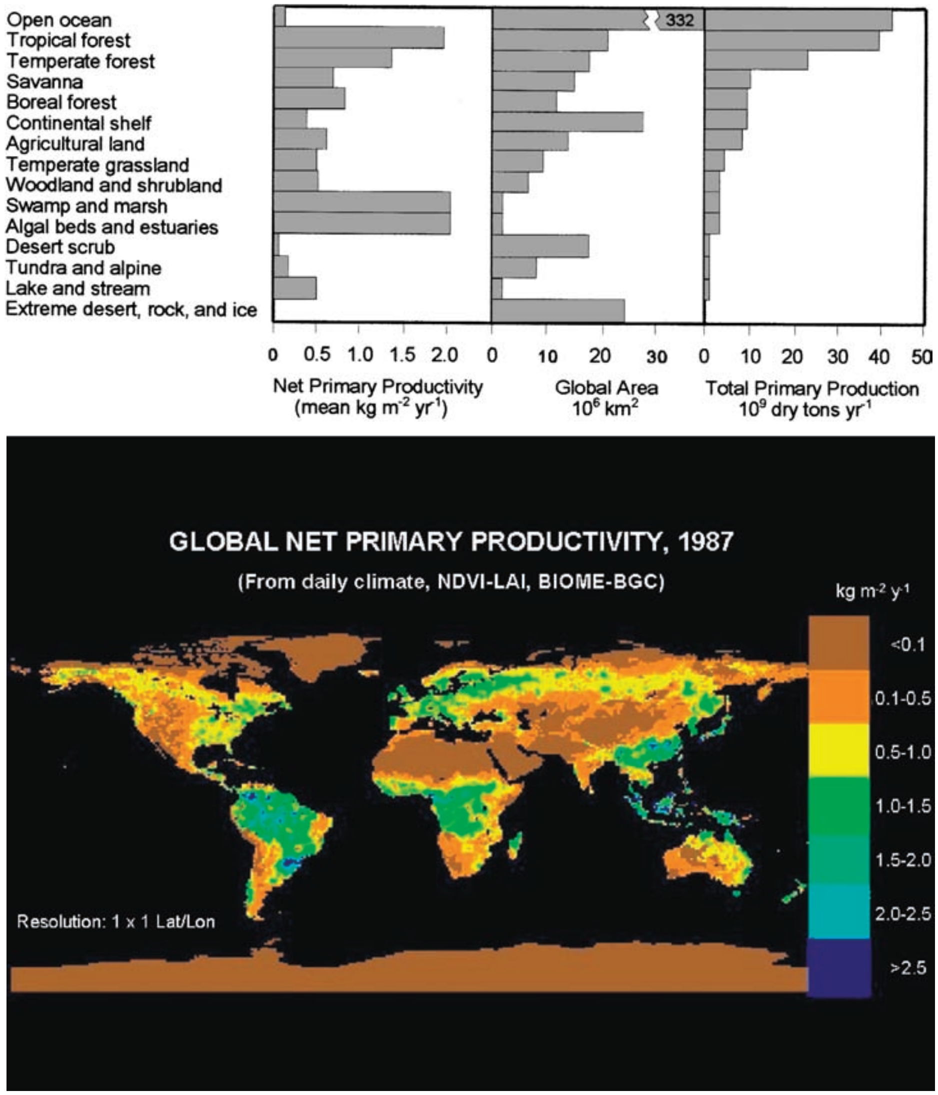


Fig. 11.4 Net primary production (NPP), total area, and contribution to global net primary production of the major biomes (*top,* data from Whittaker 1970); global calculation of total NPP using the light use efficiency model and biweekly time-integrated normalized difference vegetation index (NDVI) values for 1987 (from R. Waring and Running 1998).

from insufficient precipitation, relative to evapotranspiration. Plants respond to water deficits by closing stomata, thereby reducing O_2 and CO_2 exchange with the atmosphere. Plants subject to frequent water deficits must solve the problem of acquiring CO_2, when stomatal opening facilitates water loss. Many desert and tropical epiphyte species are able to take up and store CO_2 as malate at night (when water loss is minimal) through crassulacean acid metabolism (CAM), then carboxylate the malate (to pyruvate) and refix the CO_2 through normal photosynthesis during the day (Winter and Smith 1996, Woolhouse 1981). Although

CAM plants require high light levels to provide the energy for fixing CO_2 twice (Woolhouse 1981), desert plants often have high photosynthetic efficiencies relative to foliage biomass (W. Webb *et al.* 1983).

Air circulation is necessary to replenish CO_2 within the uptake zone neighboring the leaf surface. Although atmospheric concentrations of CO_2 may appear adequate, high rates of photosynthesis, especially in still air, can deplete CO_2 in the boundary area around the leaf, reducing photosynthetic efficiency.

Ruderal plants in terrestrial ecosystems and phytoplankton in aquatic ecosystems usually have high turnover rates (short life spans) and high rates of net primary production per gram biomass because resources are relatively nonlimiting and the plants are composed primarily of photosynthetic tissues. Net primary production by all vegetation is low, however, because of the small biomass available for photosynthesis. By contrast, later successional plant species have low turnover rates (long life spans) and lower rates of net primary production per gram because shading reduces photosynthetic efficiency and large portions of biomass necessary for support and access to sunlight are nonphotosynthetic but still respire (e.g., wood and roots).

Usually, the NPP that is consumed by herbivores on an annual basis is low, an observation that prompted Hairston *et al.* (1960) to conclude that herbivores are not resource limited and must be controlled by predators. However, early studies of energy content of plant material involved measurement of change in enthalpy (heat of combustion) rather than free energy (Wiegert 1968). We now know that the energy initially stored as carbohydrates is incorporated, through a number of metabolic pathways, into a variety of compounds varying widely in their digestibility by herbivores. The energy stored in plant compounds often costs more to digest than the free energy it provides (see Chapters 3 and 4). Many of these herbivore-deterring compounds require energy expenditure by the plant, reducing the free energy available for growth and reproduction (e.g., Coley 1986). The methods used to measure herbivory often overestimate consumption but underestimate the turnover of NPP (Risley and Crossley 1993, Schowalter and Lowman 1999; see Chapter 12).

B. Secondary Productivity

Net primary production provides the energy for all heterotrophic activity. Consumers capture the energy stored within the organic molecules of their food sources. Therefore, each trophic level acquires the energy represented by the biomass consumed from the lower trophic level. The rate of conversion of NPP into heterotroph tissues is *secondary productivity.* As with primary productivity, we can distinguish the total rate of energy consumption by secondary producers from the energy incorporated into consumer tissues (net secondary productivity) after expenditure of energy through respiration. Secondary productivity is limited by the amount of net primary production because only the net energy stored in plants is available for consumers, secondary producers cannot consume more matter than is available, and energy is lost during each transfer between trophic levels.

Not all food energy removed by consumers is ingested. Consumer feeding often is wasteful. Scraps of food are dropped, or damaged plant parts are abscissed (Faeth *et al.* 1981, Risley and Crossley 1993), making this material available to decomposers. Of the energy contained in ingested material, some is not assimilable and is egested, becoming available to reducers. A portion of assimilated energy must be used to support metabolic work (e.g., for maintenance, food acquisition, and various other activities) and is lost through respiration (see Chapter 4). The remainder is available for growth and reproduction (secondary production).

Secondary production can vary widely among heterotrophs and ecosystems. Herbivores generally have lower efficiencies of food conversion (ingestion/GPP <10%) than do predators (<15%) because the chemical composition of animal food is more digestible than is plant food (Whittaker 1970). Heterotherms have higher efficiencies than do homeotherms because of the greater respiratory losses associated with maintaining constant body temperature (Golley 1968; see also Chapter 4). Therefore, ecosystems dominated by invertebrates or heterothermic vertebrates (e.g., most freshwater aquatic ecosystems dominated by insects and fish) will have higher rates of secondary production, relative to net primary production, than will ecosystems with greater representation of homeothermic vertebrates.

Eventually, all plant and animal matter enters the detrital pool as organisms die. The energy in detritus then becomes available to reducers (detritivores and decomposers). Detritivores fragment detritus and inoculate homogenized detritus with microbial decomposers during gut passage. Detrital material consists primarily of lignin and cellulose, but detritivores often improve their efficiency of energy assimilation by association with gut microorganisms or by reingestion of feces (coprophagy) following microbial decay of cellulose and lignin (e.g., Breznak and Brune 1994).

C. Energy Budgets

Energy budgets can be developed from measurements of available solar energy, primary productivity, secondary productivity, decomposition, and respiration. Comparison of budgets and conversion efficiencies among ecosystems can indicate factors affecting energy flow and contributions to global energy budget. Development of energy budgets for agricultural ecosystems can be used to evaluate the efficiency of human resource production.

Lindeman (1942) was the first to demonstrate that ecosystem function can be represented by energy flow through a trophic pyramid or food web. He accounted for the energy stored in each trophic level, transferred between each pair of trophic levels, and lost through respiration. H. Odum (1957) and Teal (1957, 1962) calculated energy storage and rates of energy flow among trophic levels in several aquatic and wetland ecosystems (Fig. 11.5). E. Odum and Smalley (1959) and Smalley (1960) calculated energy flow through consumer populations. The International Biological Programme (IBP) focused attention on the energy budgets of various ecosystems (e.g., Bormann and Likens 1979, Misra 1968, E. Odum

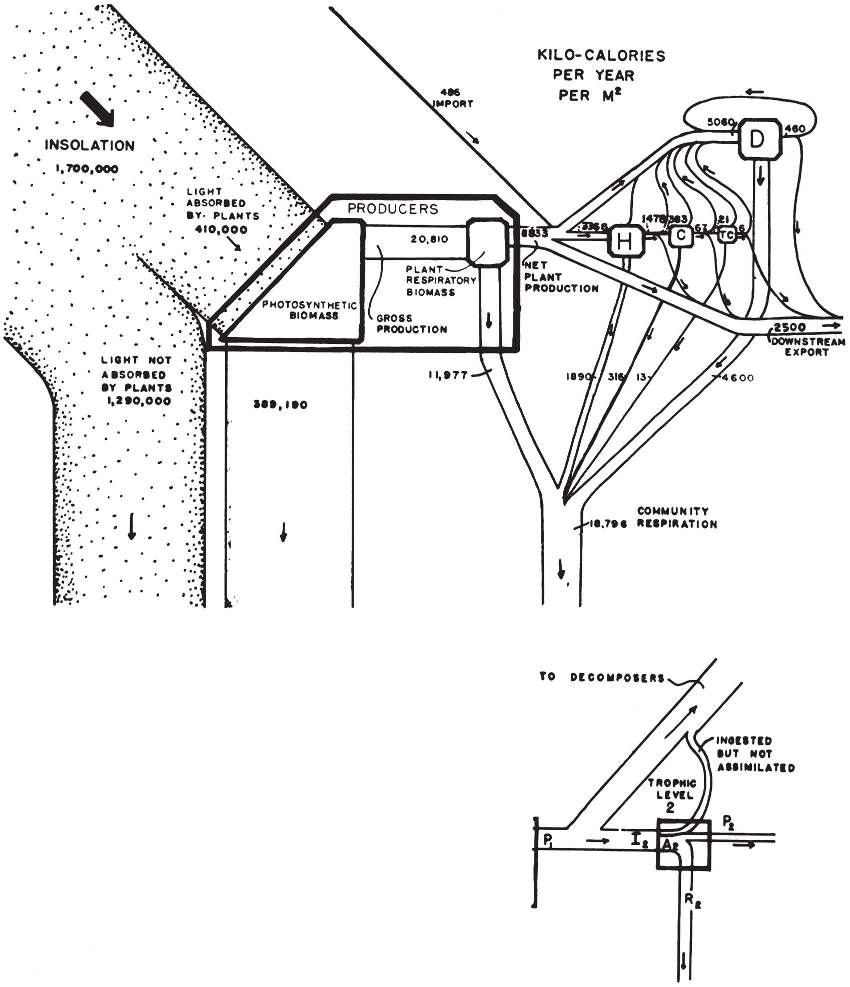


Fig. 11.5 Energy flow (kcal m^{-2} yr^{-1}) in the Silver Springs ecosystem. H, herbivores; C, predators; TC, top predators; D, decomposers. From H. Odum (1957) with permission from the Ecological Society of America.

1969, Petrusewicz 1967, Sims and Singh 1978), including energy flow through insect populations (Kaczmarek and Wasilewski 1977, McNeill and Lawton 1970, Reichle and Crossley 1967).

More recently, the energy budgets of agricultural ecosystems have been evaluated from the standpoint of energetic efficiency and sustainability. Whereas the energy available to natural communities comes from the sun, additional energy inputs are necessary to maintain agricultural productivity. These include energy from fossil fuels (used to produce fertilizers and pesticides and to power machinery) and from human and animal labor (Bayliss-Smith 1990, Schroll 1994). These additional inputs of energy have been difficult to quantify (Bayliss-Smith 1990). Although the amount and value of food production is well-known, the efficiency of food production (energy content of food produced per unit of energy input) is poorly known but critical to sustainability and economic development (Patnaik and Ramakrishnan 1989). Promotion of predaceous insects to control pests, as an alternative to energy-expensive pesticides, and of soil organisms (including insects) to reduce loss of soil organic matter, as an alternative to fertilizers, has been proposed as a means to increase efficiency of agricultural production (Elliott *et al.* 1984, Ostrom *et al.* 1997).

Costanza *et al.* (1997), Daily (1997), N. Myers (1996), and H. Odum (1996) attempted to account for all energy used to produce and maintain the goods and services that support human culture. In addition to the market and energy value of current ecosystem resources, energy was expended in the past to produce those resources. The energy inputs, over time, that produced biomass must be included in the energy value of the system. When forests are harvested, the energy or resources derived from the timber can be replaced only by cumulative inputs of solar energy to replace the harvested biomass. Additional energy is expended for transportation of resources to population centers and development of societal infrastructures. Solar energy also generates tides and evaporates water necessary for maintenance of intertidal and terrestrial ecosystems and their resources.

H. Odum (1996) proposed the term *emergy* to denote the total amount of energy used to produce resources and cultural infrastructures. Costanza *et al.* (1997), Daily (1997), and H. Odum (1996) note that ecosystems provide a variety of “free” services, such as filtration of air and water, pollination, and fertilization of floodplains, with energy derived from the sun and from topographic gradients, that must be replaced at the cost of fossil fuel expenditure when these services are lost as a result of environmental degradation (e.g., channelization and impoundment of streams). Sustainability of systems based on ecosystem resources thus depends on the energy derived from the ecosystem relative to the total emergy required to produce the resources. Consequently, many small-scale subsistence agricultural systems are far more efficient and sustainable than are larger-scale, industrial agricultural systems that could not be sustained without massive inputs from nonrenewable energy sources. Unfortunately, these more sustainable agroecosystems may not provide sufficient production to feed the growing world population.

III. BIOGEOCHEMICAL CYCLING

Organisms use the energy available to them as currency to acquire, concentrate, and organize chemical resources for growth and reproduction (Sterner and Elser 2002; see Chapter 4). Even sedentary organisms living in or on their material resources must expend energy to acquire resources against chemical gradients or to make these resources useable (e.g., through oxidation and reduction reactions necessary for digestion and assimilation). Energy gains must be greater than energy expenditures, or resource acquisition, growth, and reproduction cannot be maintained.

Energy and matter are transferred from one trophic level to the next through consumption; however, whereas energy is dissipated ultimately as heat, matter is conserved and reused. Conservation and reuse of nutrients within the ecosystem buffer organisms against resource limitation and contribute to ecosystem stability. The efficiency with which limiting elements are recycled varies among ecosystems. Biogeochemical cycling results from fluxes among biotic and abiotic storage pools.

Biogeochemical cycling occurs over a range of spatial and temporal scales. Cycling occurs within ecosystems as a result of trophic transfers and recycling of biotic materials made available through decomposition. Rapid cycling by microbial components is coupled with slower cycling by larger, longer-lived organisms within ecosystems. Nutrients exported from one ecosystem become inputs for another. Detritus washed into streams during storms is the primary source of nutrients for many stream ecosystems. Nutrients moving downstream are major sources for estuarine and marine ecosystems. Nutrients lost to marine sediments are returned to terrestrial pools through geologic uplifting. Materials stored in these long-term abiotic pools become available for extant ecosystems through weathering and erosion. The pathways and rates of nutrient movement can be described by ecological stoichiometry (Sterner and Elser 2002).

A. Abiotic and Biotic Pools

The sources of all elemental nutrients necessary for life are abiotic pools, the atmosphere, oceans, and sediments. The atmosphere is the primary source of nitrogen, carbon (as carbon dioxide), and water for terrestrial ecosystems. Sediments are a major pool of carbon (as calcium carbonate), as well as the primary source of mineral elements (e.g., phosphorus; sulfur; and cations such as sodium, potassium, calcium, and magnesium released through chemical weathering). The ocean is the primary source of water, but it also is a major source of carbon (from carbonates) for marine organisms and of cations that enter the atmosphere when winds >20 kph lift water and dissolved minerals from the ocean surface.

Resources from abiotic pools are not available to all organisms but must be transformed (fixed) into biologically useful compounds by autotrophic organisms. Photosynthetic plants acquire water and atmospheric or dissolved carbon dioxide to synthesize carbohydrates, which then are stored in biomass. Nitrogen-fixing bacteria and cyanobacteria acquire atmospheric or dissolved N_2 and convert it into ammonia, which they and some plants can incorporate directly into amino acids and nucleic acids. Nitrifying bacteria oxidize ammonia into nitrite and nitrate, the form of nitrogen available to most plants. These autotrophs also acquire other essential nutrients in dissolved form. The living and dead biomass of these organisms represents the pool of energy and nutrients available to heterotrophs.

The size of biotic pools represents storage capacity that buffers the organisms representing these pools against reduced availability of nutrients from abiotic sources. Larger organisms have a greater capacity to store energy and nutrients for use during periods of limited resource availability than do smaller organisms. Many plants can mobilize stored nutrients from tubers, rhizomes, or woody tissues to maintain metabolic activity during unfavorable periods. Similarly, larger animals can store more energy, such as in the fat body of insects, and can retrieve nutrients from muscle or other tissues during periods of inadequate resource acquisition. Detritus represents a major pool of organic compounds. The nutrients from detritus become available to organisms through decomposition. Ecosystems with greater nutrient storage in living or dead biomass tend to be more resistant to certain environmental changes than are ecosystems with more limited storage capacity (Webster *et al.* 1975).

B. Major Cycles

The biota modifies chemical fluxes. In the absence of biota, the rate and direction of chemical fluxes would be controlled solely by the physical and chemical factors determining exchanges between abiotic pools. Chemicals would be retained at a site only to the extent that chelation or concentration gradients restricted leaching or diffusion. Exposed nutrients would continue to move with wind or water (erosion). Biotic uptake and storage of chemical resources creates a biotic pool that reduces chemical storage in abiotic pools, altering rates of exchange among abiotic pools and restricting movement of nutrients across chemical and topographic gradients. For example, the uptake and storage of atmospheric CO_2 by plants (including long-term storage in fossil biomass, i.e., coal, oil and gas) and the uptake and storage of calcium carbonate by marine animals (and deposition in marine sediments) control concentration gradients of CO_2 available for exchange between the atmosphere and ocean (Keeling *et al.* 1995, Sarmiento and Le Quéré 1996). Conversely, fossil fuel combustion, deforestation and desertification, and destruction of coral reefs are reducing CO_2 uptake by biota and releasing CO_2 from biotic storage, thereby increasing global CO_2 available for exchange between the atmosphere and ocean. Biotic uptake of various sedimentary nutrients retards their transport from higher elevations back to marine sediments.

Consumers, including insects, affect the rate at which nutrients are acquired and stored (see Chapters 12–14). Consumption reduces the biomass of the lower trophic level, thereby affecting nutrient uptake and storage at that trophic level, and moves nutrients from consumed biomass into biomass at the higher trophic level (through secondary production) or into the detritus (through secretion and excretion) where nutrients become available to detritivores and soil microorganisms or are exported via water flow to aquatic food webs. Nutrients are recycled through decomposition of dead plant and animal biomass, which releases simple organic compounds or elements into solution for reacquisition by autotrophs.

Some nutrients are lost during trophic transfers. Carbon is lost (exported) from ecosystems as CO_2 during respiration. Gaseous or dissolved CO_2 remains available to organisms in the atmosphere and oceanic pools. Organic biomass can be blown or washed away. Soluble nutrients are exported as water percolates through the ecosystem and enters streams. The efficiency with which nutrients are retained within an ecosystem reflects their relative availability. Nutrients such as nitrogen and phosphorus often are limiting and tend to be cycled and retained in biomass more efficiently than are nutrients that are more consistently available, such as potassium and calcium. The following four examples exemplify the processes involved in biogeochemical cycling.

1. Hydric Cycle

Water availability, as discussed in Chapters 2 and 9, is one of the most important factors affecting the distribution of terrestrial organisms. Many organisms are modified to optimize their water balances in arid ecosystems (e.g., through their adaptations for acquiring and retaining water; Chapter 2). Water available to plants is a primary factor affecting photosynthesis and ecosystem energetics (see earlier in this chapter). Water absorbs solar energy, with little change in temperature, thereby buffering humid ecosystems against large changes in temperature. At the same time, water use by organisms significantly affects its passage through terrestrial ecosystems.

The primary source of water for terrestrial ecosystems is water vapor from evaporation over the oceans (Fig. 11.6). The availability of water to terrestrial ecosystems is controlled by a variety of factors, including the rate of evaporation from the ocean, the direction of prevailing winds, atmospheric and topographic factors that affect convection and precipitation, temperature, relative humidity, and soil texture. Water enters terrestrial ecosystems as precipitation and condensation and as subsurface flow and groundwater derived from precipitation or condensation at higher elevations. Condensation may be a major avenue for water input to arid ecosystems. Many plants in arid regions are adapted to acquire

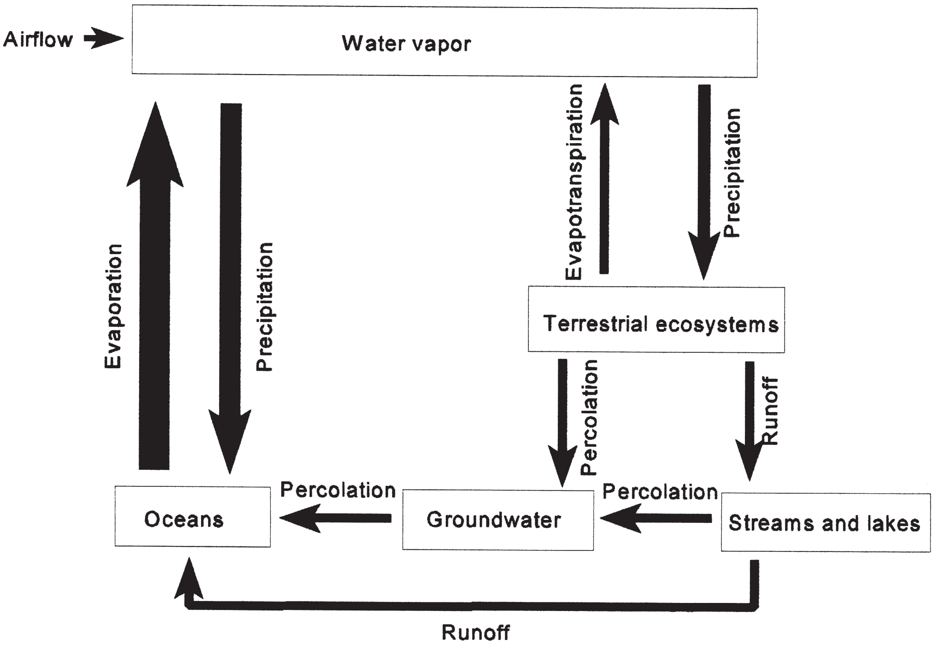


Fig. 11.6 The hydric cycle. Net evaporation over the oceans is the source of water vapor carried inland by air currents. Water precipitated into terrestrial ecosystems eventually is returned to the ocean.

water through condensation. Some desert insects also acquire water through condensation on specialized hairs or body parts (R. Chapman 1982). Vegetation intercepts up to 50% of precipitation, depending on crown structure and plant surface area (G. Parker 1983). Most intercepted water evaporates. The remainder penetrates the vegetation as throughfall (water dripping from foliage) and stemflow (water funneled to stems).

Vegetation takes up water primarily from the soil, using some in the synthesis of carbohydrates. Vascular plants conduct water upward and transpire much of it through the stomata. Evapotranspiration is the major mechanism for maintaining the upward capillary flow of water from the soil to the canopy. This active evaporative process greatly increases the amount of water moving back into the atmosphere, rather than flowing downslope, and may increase the availability of water for precipitation at a particular site, as discussed later in this chapter.

Vegetation stores large amounts of water intracellularly and extracellularly and controls the flux of water through the soil and into the atmosphere. Accumulation of organic material increases soil water storage capacity and further reduces downslope flow. Soil water storage mediates plant acquisition of other nutrients in dissolved form. Food passage through arthropods and earthworms, together with materials secreted by soil microflora, bind soil particles together, forming soil aggregates (Hendrix *et al.* 1990, Setälä *et al.* 1996). These aggregates increase water and nutrient storage capacity and reduce erosibility. Burrowing organisms increase the porosity and water storage capacity of soil and decomposing wood (e.g., earthworms and wood borers) (e.g., Eldridge 1994). Macropore flow increases the rate and depth of water infiltration.

Some organisms also control water movement in streams. Swamp and marsh vegetation restricts water flow in low-gradient ecosystems. Trees falling into stream channels impede water flow. Similarly, beaver dams impede water flow and store water in ponds. However, water eventually evaporates or reaches the ocean, completing the cycle.

2. Carbon Cycle

The carbon cycle (Fig. 11.7) is particularly important because of its intimate association with energy flow, via the transfer of chemical energy in carbohydrates, through ecosystems. Carbon is stored globally both as atmospheric carbon dioxide and as sedimentary and dissolved carbonates (principally calcium carbonate). The atmosphere and ocean mediate the global cycling of carbon among terrestrial and aquatic ecosystems. The exchange of carbon between atmosphere and dissolved or precipitated carbonates is controlled by temperature, carbonate concentration, salinity, and biological uptake that affects concentration gradients (Keeling *et al.* 1995, Sarmiento and Le Quéré 1996).

Carbon enters ecosystems primarily as a result of photosynthetic fixation of CO_2 in carbohydrates. The chemical energy stored in carbohydrates is used to synthesize all the organic molecules used by plants and animals. Carbon enters many aquatic ecosystems, especially those with limited photosynthesis, primarily as allochthonus inputs of exported terrestrial materials (e.g., terrestrial organisms captured by aquatic animals, detritus, and dissolved organic material entering

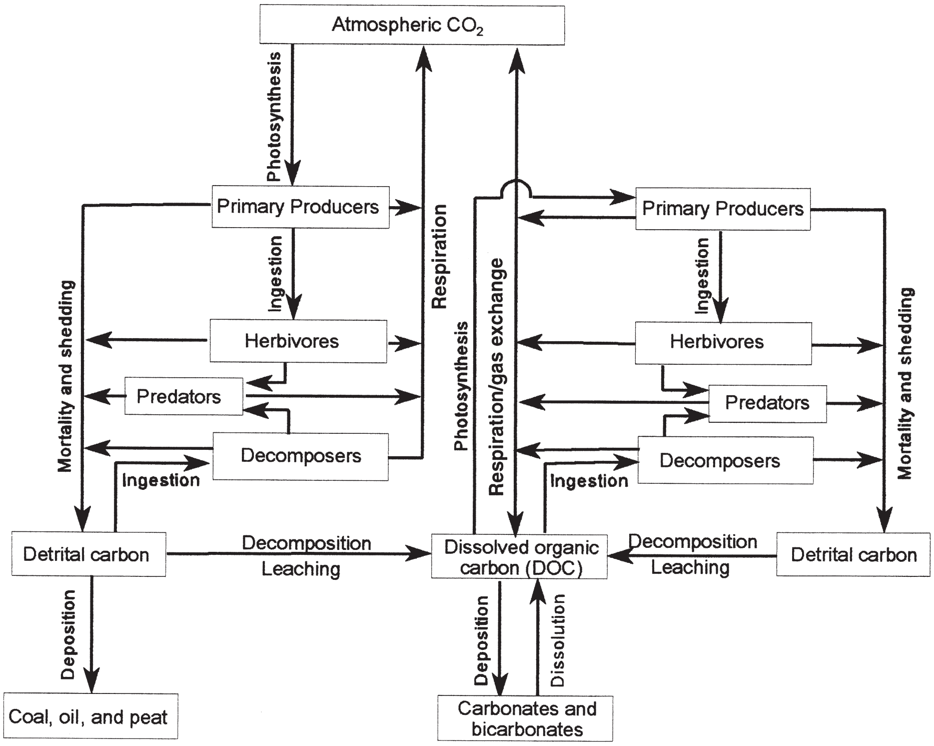


Fig. 11.7 The global carbon cycle. The atmosphere is the primary source of carbon for terrestrial ecosystems (*left*), whereas dissolved carbonates and bicarbonates are the primary source of carbon for marine ecosystems (*right*). Exchange of carbon between atmosphere, hydrosphere, and geosphere is regulated largely by biotic uptake and deposition.

with runoff or leachate). Carbon is transferred among trophic levels through consumption, converted into an astounding diversity of compounds for a variety of uses, and eventually is returned to the atmosphere as CO_2 from respiration, especially during decomposition of dead organic material, completing the cycle. However, loss of carbon from an ecosystem is minimized by rapid acquisition and immobilization of soluble and fine particulate carbon by soil organisms and aquatic filter feeders, from which carbon becomes available for transfer within soil and aquatic food webs (de Ruiter *et al.*, 1995, J. Wallace and Hutchens 2000).

However, some carbon compounds (especially complex polyphenols, e.g., lignin) decompose very slowly, if at all, and are stored for long periods as soil organic matter, peat, coal, or oil. Humic compounds are phenolic polymers that are resistant to chemical decomposition and constitute long-term carbon storage in terrestrial soils. These compounds contribute to soil water and nutrient-holding capacities because of their large surface area and numerous binding sites. Plants produce organic acids that are secreted into the soil through roots. These acids facilitate extraction of mineral nutrients from soil exchange sites, maintain ionic balance (with mineral cations), reduce soil pH, and often inhibit decomposition of organic matter. Similarly, peat accumulates in bogs where low pH inhibits decomposition and eventually may be buried, contributing to formation of coal or oil. Coal and oil represent long-term storage of accumulated organic matter that decomposed incompletely as a result of burial, anaerobic conditions, and high pressure. The carbon removed from the atmosphere by these fossil plants is now reentering the atmosphere rapidly, as a result of fossil fuel combustion, leading to increased atmospheric concentrations of CO_2.

3. *Nitrogen Cycle*

Nitrogen is a critical element for synthesis of proteins and nucleic acids and is available in limited amounts in most ecosystems. The atmosphere is the reservoir of elemental nitrogen, making nitrogen an example of a nutrient with an atmospheric cycle (Fig. 11.8). Most organisms cannot use gaseous nitrogen and many other nitrogen compounds. In fact, some common nitrogen compounds are toxic in small amounts to most organisms (e.g., ammonia). Nitrogen cycling is mediated by several groups of microorganisms that transform toxic or unavailable forms of nitrogen into biologically useful compounds.

Gaseous N_2 from the atmosphere becomes available to organisms through fixation in ammonia, primarily by nitrogen-fixing bacteria and cyanobacteria. These organisms are key components of most ecosystems but are particularly important in ecosystems subject to periodic massive losses of nitrogen, such as through fire. Many early successional plants, especially in fire-dominated ecosystems, have symbiotic association with nitrogen-fixing bacteria in root nodules. These plants can use the ammonia produced by the associated bacteria, but most plants require nitrate (NO_3) as their source of nitrogen.

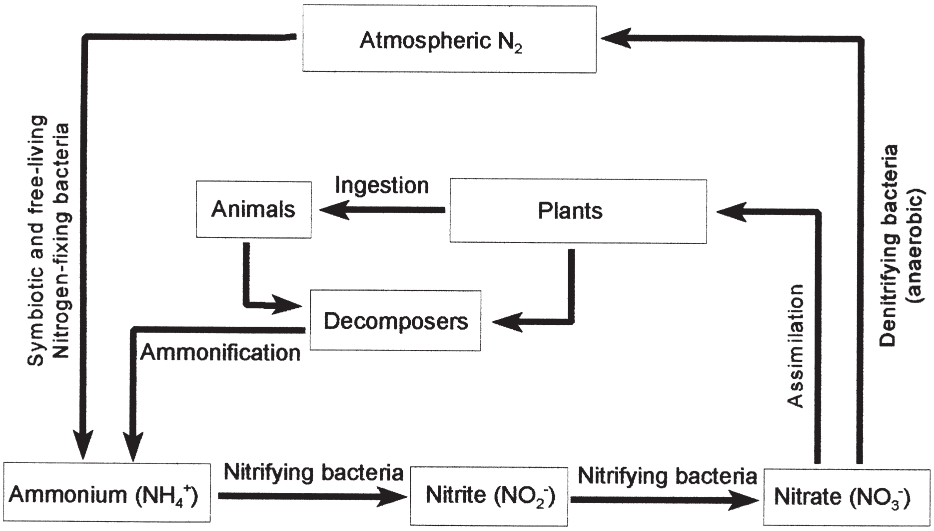


Fig. 11.8 The nitrogen cycle. Bacteria are the primary organisms responsible for transforming elemental nitrogen into forms available for assimilation by plants. Note that the return of nitrogen to the atmospheric pool occurs almost exclusively under anaerobic conditions.

Ammonium compounds also are produced by lightning and volcanic eruptions. Nitrifying bacteria oxidize ammonia to nitrite (NO_2) and nitrate, which then is available to plants for synthesis of amino acids and nucleic acids and transferred to higher trophic levels through consumption. The nitrogen compounds in dead organic matter are decomposed to ammonium by ammonifying bacteria. Organic nitrogen enters aquatic ecosystems as exported terrestrial organisms, detritus, or runoff and leachate solutions. Nitrogen in freshwater ecosystems similarly is transferred among trophic levels through consumption, eventually reaching marine ecosystems. Under anaerobic conditions, which occur naturally and as a result of anthropogenic eutrophication or soil compaction, the biotic cycle can be disrupted by anaerobic denitrifying bacteria that convert nitrate to gaseous nitrogen, which is lost to the atmosphere, thereby completing the cycle. However, nitrogen loss is minimized by soil organisms that aerate the soil through excavation and by the rapid acquisition and immobilization of soluble nitrogen by soil microorganisms and aquatic filter feeders, from which nitrogen becomes available to plants and to soil and aquatic food webs.

4. Sedimentary Cycles

Many nutrients, including phosphorus and mineral cations, are available only from sedimentary sources. These nutrients are cycled in similar ways, as exemplified by phosphorus (Fig. 11.9). Phosphorus is biologically important in molecules that mediate energy exchange during metabolic processes (adenosine triphosphate [ATP] and adenosine diphosphate [ADP]) and in phospholipids. Like nitrogen, it is available to organisms only in certain forms and is in limiting supply in most ecosystems. Phosphorus and mineral cations become available to terrestrial ecosystems as a result of chemical weathering or erosion of geologically uplifted, phosphate-bearing sediments.

Phosphate enters an ecosystem from weathered bedrock and moves among terrestrial ecosystems through materials washed downslope or filtered from the air. Phosphorus is highly reactive but available to plants only as phosphate, which often is bound to soil particles. Plants extract phosphorus (and mineral cations) from cation exchange and sorption sites on soil particles and from soil solution. Phosphorus then is synthesized into biological molecules and transferred to higher trophic levels through consumption; it eventually is returned to the soil as dead organic matter and is decomposed. Phosphorus enters aquatic ecosystems largely in particulate forms exported from terrestrial ecosystems. It is transferred between aquatic trophic levels through consumption, eventually being deposited in deep ocean sediments, completing the cycle. Phosphorus loss is minimized by soil organisms and aquatic filter feeders, which rapidly acquire and immobilize soluble phosphorus and make it available for plant uptake and exchange among soil and aquatic organisms.

C. Factors Influencing Cycling Processes

A number of factors alter the rates and pathways of biogeochemical fluxes. Variation in fluxes reflects the chemical properties and source of the nutrient;

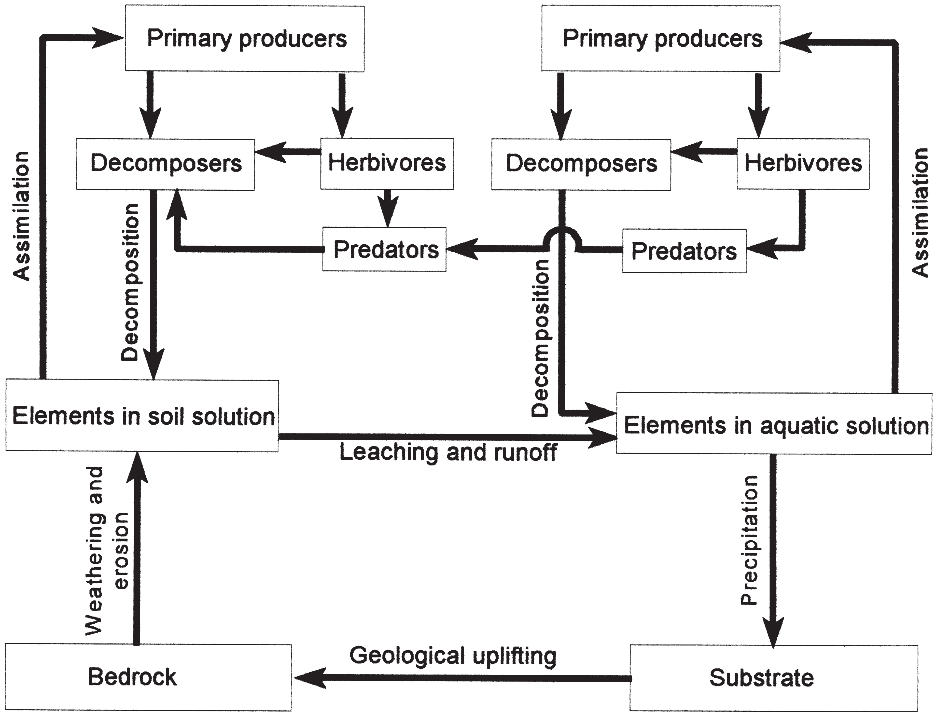


Fig. 11.9 Sedimentary cycle. Phosphorus and other nongaseous nutrients precipitate from solution and are stored largely in sediments of marine origin. These nutrients become available to terrestrial ecosystems primarily through chemical weathering of uplifted sediments.

interactions with other cycles; and the composition of the community, especially the presence of specialized organisms that control particular fluxes. Hence, changes in community composition resulting from disturbance and recovery alter the rates and pathways of chemical fluxes.

The chemical properties of various elements and compounds, especially their solubility and susceptibility to pH changes, and biological uses affect cycling behavior. Some elements, such as Na and K, form compounds that are readily soluble over normal ranges of pH. These elements generally have high rates of input to ecosystems via precipitation but also high rates of export via runoff and leaching. Other elements, such as Ca and Mg, form compounds that are not as soluble over usual ranges of pH and have lower rates of input and export. Elements such as nitrogen and phosphorus are necessary for all organisms, relatively limiting, and generally conserved within organisms. For example, deciduous trees usually resorb nitrogen from senescing foliage prior to leaf fall (Marschner 1995). Sodium has no known function in plants and is not retained in plant tissues, but it is required by animals for osmotic balance and for muscle and nerve function. Consequently, it is conserved tightly by these organisms. In fact, animals often seek mineral sources of sodium (e.g., Seastedt and Crossley 1981b). Many decay fungi accumulate sodium (Cromack *et al.* 1975, Schowalter *et al.* 1998), despite absence of apparent use in fungal metabolism, perhaps to attract animal vectors of fungal spores.

Biogeochemical cycles interact with each other in complex ways (Daufresne and Loreau 2001, Elser and Urabe 1999, Rastetter *et al.* 1997, Sterner and Elser 2002). For example, precipitation affects decomposition and carbon storage in soils (Schuur *et al.* 2001). Some plants respond to increased atmospheric CO_2 by reducing stomatal opening, thereby acquiring sufficient CO_2 while reducing water loss. Hence, increased size of the atmospheric pool of CO_2 may alter transpiration, permitting some plant species to colonize more arid habitats. Similarly, the calcium cycle interacts with cycles of several other elements. Calcium carbonate generally accumulates in arid soils as soil water evaporates. Acidic precipitation, such as resulting from industrial emission of nitrous oxides and sulfur dioxide into the atmosphere, dissolves and leaches calcium carbonate from soils and sediments. Soils with high content of calcium carbonate are relatively buffered against pH change, whereas soils depleted of calcium carbonate become acidic, increasing export (through leaching) of other cations as well.

Some biogeochemical fluxes are controlled by particular organisms. The nitrogen cycle depends on several groups of microorganisms that control the transformation of nitrogen among various forms that are available or unavailable to other organisms (see earlier in this chapter). Soil biota secrete substances that bind soil particles into aggregates that facilitate retention of soil water and nutrients. Some plants (e.g., western redcedar, *Thuja plicata,* and dogwoods, *Cornus* spp.) accumulate calcium in their tissues (Kiilsgaard *et al.* 1987) and generally increase pH and buffering capacity of surrounding soils. Their presence or absence thereby affects retention of other nutrients, as well. Oaks, *Quercus* spp., and spruces, *Picea* spp., emit large amounts of carbon as volatile isoprene that affects the oxidation potential of the atmosphere (Lerdau *et al.* 1997). Changes in community composition following disturbance or during succession affect rates and pathways of biogeochemical fluxes. Early successional communities frequently are inefficient because of limited competition for resources by the small biomass, and early successional species have little selective pressure to retain nutrients. For example, the early successional tropical tree, *Cecropia* spp., has large, thin leaves that transpire water more rapidly than the smaller, more sclerotized leaves of later successional species. Although later successional communities are not always efficient, declining resource supply relative to growing biomass promotes efficiency of nutrient retention within the ecosystem (E. Odum 1969, Schowalter 1981).

Agricultural and silvicultural systems are inefficient largely because communities composed of a single, or few, plant species cannot acquire or retain all available forms of matter effectively. Furthermore, the diversity of organisms in natural systems may increase per capita resource acquisition or provide overall resistance to herbivores and pathogens (Cardinale *et al.* 2002, A. Hunter and Arssen 1988). Nitrogen fixation often is controlled by noncommercial species, such as symbiotic nitrogen-fixing lichens, herbs and shrubs, or structures such as large decomposing woody litter, that are suppressed or eliminated by management activities. Necessary nitrogen then must be supplied anthropogenically, often in excess amounts that leach into groundwater and streams. Exotic species also can alter nutrient cycling processes. Liu and Zou (2002) reported that invasion of tropical pastures and wet forest in Puerto Rico by exotic earthworms significantly increased decomposition rates.

IV. CLIMATE MODIFICATION

Although most previous studies have emphasized the effect of climate on survival, population growth, and distribution of organisms (see Chapters 2, 6, and 9), communities of organisms also modify local and regional climatic conditions, perhaps influencing global climatic gradients (T. Chase *et al.* 1996, J. Foley *et al.* 2003, G. Parker 1995, Pielke and Vidale 1995). Climate modification largely reflects the capacity of vegetation to shade and protect the soil surface, abate airflow, and control water fluxes (Fig. 11.10). Isoprene emission by some plant species apparently increases leaf tolerance to high temperatures and also affects the oxidation potential of the atmosphere (Lerdau *et al.* 1997). Biomes and successional stages vary widely in ability to modify climate.

When vegetation development is limited or moisture is limited, as in deserts, the soil surface is exposed fully to sunlight and contains insufficient water to restrict temperature change (T. Lewis 1998). The reflectivity of the soil surface (albedo) determines absorption of solar energy and heat. Soils with high organic content have lower albedo (0.10) than does desert sand (0.30) (Monteith 1973). Albedo also declines with increasing soil water content. In the absence of vegetation cover, surface temperatures can reach 60–70°C during the day (e.g.,

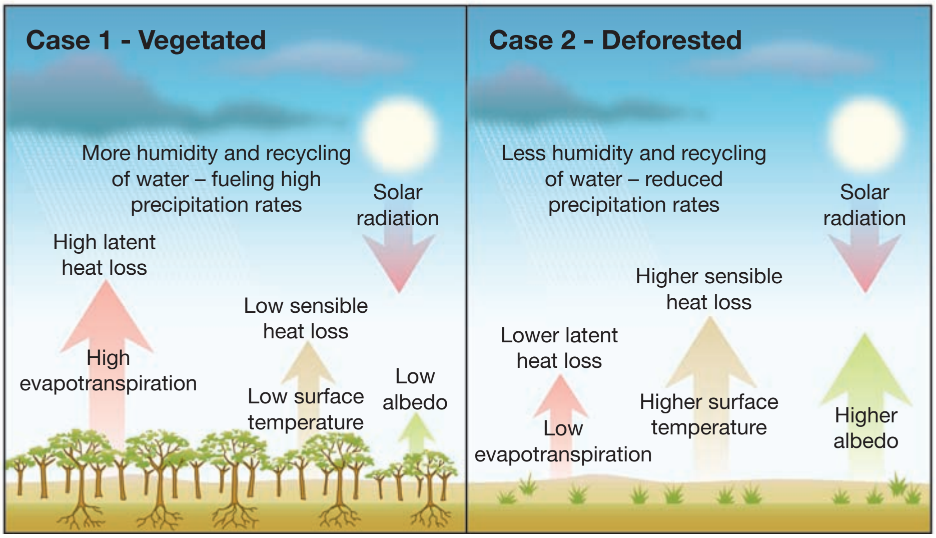


Fig. 11.10 Diagrammatic representation of the effects of vegetation on climate and atmospheric variables. The capacity of vegetation to modify climate depends on vegetation density and vertical height and complexity. From J. Foley *et al.* (2003) with permission of the Ecological Society of America. Please see extended permission list pg 571.

Seastedt and Crossley 1981a) but fall rapidly at night as a result of long-wavelength (infrared) radiation from the surface. Exposure to high wind speeds dries soil and moves soil particles into the atmosphere. Soil desiccation reduces infiltration of precipitation, leading to greater runoff and erosion. These altered soil characteristics affect albedo and precipitation patterns.

Vegetation modifies local climate conditions in several ways. Even the thin (3 mm) biological crusts, composed of cyanobacteria, green algae, lichens, and mosses, on the surface of soils in arid and semiarid regions are capable of substantially modifying surface conditions and reducing erosion (Belnap and Gillette 1998). During the day, vegetation shades the surface, reducing temperature (T. Lewis 1998). The effect of vegetation on albedo depends on vegetation structure and soil condition. Vegetation absorbs solar radiation to drive evapotranspiration (G. Parker 1995). Albedo is inversely related to vegetation height and "roughness" (the degree of unevenness of canopy topography), declining from 0.25 for vegetation <1.0 m in height to 0.10 for vegetation >30 m height; albedo generally reaches lowest values in vegetation with an uneven canopy surface (e.g., tropical forest) and highest values in vegetation with a smooth canopy surface (e.g., agricultural crops) (Monteith 1973). Canopy roughness creates turbulence in air flow, thereby contributing to surface cooling by wind (sensible heat loss) and by evapotranspiration (latent heat loss) (J. Foley *et al.* 2003). At night, the canopy absorbs reradiated infrared energy from the ground, maintaining warmer nocturnal temperatures, compared to nonvegetated areas. Canopy cover intercepts precipitation and can reduce the impact of rain drops on the soil surface (Fig. 11.11, Meher-Homji 1991, Ruangpanit 1985), although this effect depends on rainfall volume and droplet size (Calder 2001). Vegetation impedes the downslope movement of water, thereby reducing erosion and loss of soil. Soil organic matter retains water, increasing soil moisture capacity and reducing temperature change. Exposure of individual organisms to damaging or lethal wind speeds is reduced as a result of buffering by surrounding individuals.

The degree of climate modification depends on vegetation density and vertical structure. Sparse vegetation has less capacity to modify temperature, water flow, and wind speed than does dense vegetation. Shorter vegetation traps less radiation between multiple layers of leaves and stems and modifies climatic conditions within a shorter column of air compared to taller vegetation. Tall, multicanopied forests have the greatest capacity to modify local and regional climate because the stratified layers of foliage and denser understory successively trap filtered sunlight, intercept precipitation and throughfall, contribute to evapotranspiration, and impede airflow in the deepest column of air. G. Parker (1995) demonstrated that rising temperatures during midday had the greatest effect in upper canopy levels in a temperate forest (Fig. 11.12). Temperature between 40 and 50 m height ranged from 16°C at night to 38°C during mid-afternoon (a diurnal fluctuation of 22°C); relative humidity in this canopy zone declined from >95% at night to 50% during mid-afternoon. Below 10 m, temperature fluctuation was only 10°C and relative humidity was constant at >95%. Windsor (1990) reported similar gradients in canopy environment in a lowland tropical forest.

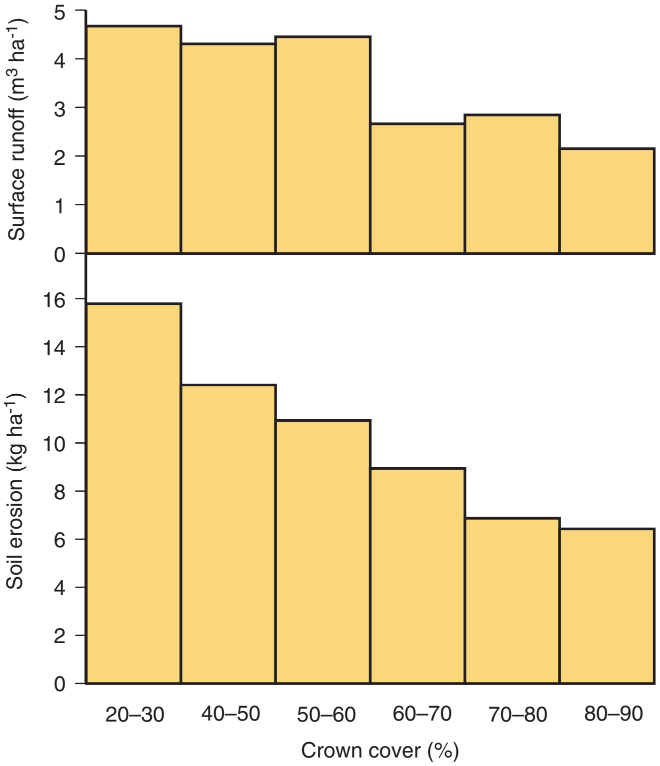


Fig. 11.11 Effect of canopy cover on average runoff and soil erosion, based on 41 runoff-producing storms totaling 1128 mm in northern Thailand. Data from Ruangpanit (1985).

Furthermore, evapotranspiration can affect local and regional precipitation. Salati (1987) reported that 30% of precipitation in tropical rainforests in the Amazon basin was generated locally by evapotranspiration. Local recycling of water may be most pronounced in montane areas, where steep vertical temperature gradients condense rising evapotranspired water.

Insects and other organisms (including humans) alter vegetation and soil structure (Fig. 11.13) and thereby affect biotic control of local and regional climate (see Chapters 12–14). Deforestation or desertification reduce evapotranspirative cooling, offsetting the effect of increased albedo, thereby increasing surface temperatures and reducing precipitation and relative humidity (J. Foley *et al.* 2003, T. Lewis 1998, Salati 1987). Costa and Foley (2000) calculated a net warming of 1–2°C in tropical regions as a result of deforestation, an effect that would exacerbate the warming resulting from increased atmospheric CO_2. Forest fragmentation increases wind fetch and penetration of air from surrounding crop or pasture zones into forest fragments (J. Chen *et al.* 1995). Belnap and Gillette (1998) found that trampling disturbance of the brittle biological crusts on desert soils greatly increased the effect of wind on soil loss. Increased levels of airborne particulates reduce the penetration of photosynthetically active radiation.

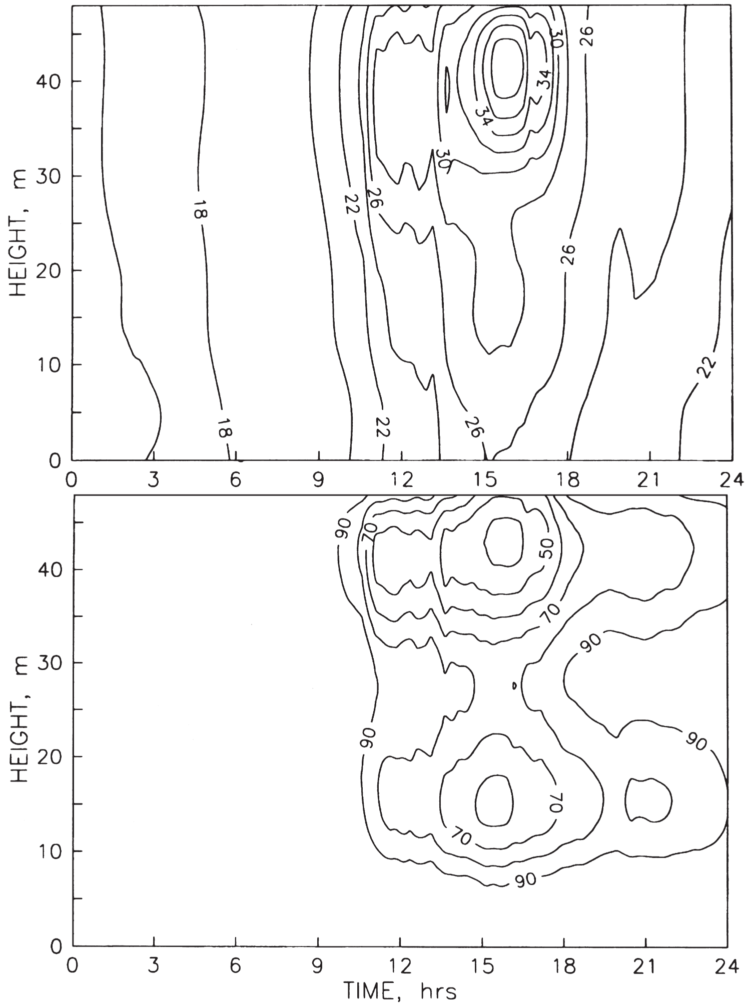


Fig. 11.12 Height-time profiles of air temperature and relative humidity in a mixed-hardwood forest in Maryland. Temperature contours are 2°C; relative humidity contours are 10% units. Nocturnal temperature gradients are weak, but a hot spot develops in the upper canopy in mid-afternoon. Humidity declined in the upper canopy in mid-afternoon, coincident with peak temperatures, and was near saturation (>95%) outside the marked contours. From G. Parker (1995). Please see extended permission list pg 571.

Deforestation and desertification could initiate positive feedback between climate and vegetation change. Holocene warming led to northward advance of the boreal forest, which lowered albedo and contributed to continued warming of the ecotone (J. Foley *et al.* 1994). Schlesinger *et al.* (1990) reported that desertification results in a destabilizing positive feedback, whereby initial vegetation removal causes surface warming and drying that stresses and kills adjacent vegetation, leading to an advancing arc of desertified land. The effects of similar, large-scale vegetation changes resulting from insect outbreaks on climatic conditions have not been evaluated.

Fig. 11.13 Deforestation in Panamá. Removal of tropical rainforest cover has exposed soil to solar heating and severe erosion, leading to continued ecosystem deterioration and, potentially, to altered regional temperature and precipitation patterns.

V. ECOSYSTEM MODELING

Modeling has become a useful tool for testing hypotheses concerning behavior and self-regulation of complex systems (e.g., Camilo and Willig 1995, B. Patten 1995, Ulanowicz 1995) and for predicting ecosystem responses to environmental changes, as well as ecosystem contributions to environmental change, especially carbon flux (e.g., Rastetter *et al.* 1991, Sarmiento and Le Quéré 1996). The logistical difficulty of measuring and manipulating all ecosystem components and processes for experimental purposes has placed greater emphasis on modeling to simulate experimental conditions and to identify critical components and processes for further study.

Modeling at the ecosystem level necessarily starts with conceptual models of linkages among components and reflects the perception of individual modelers of the importance of particular components and interactions (e.g., Figs. 1.3, 11.6–11.9). Models differ in the degree to which species are distinguished in individual submodels or combined into functional group submodels (de Ruiter *et al.* 1995, Naeem 1998, Polis 1991b, Reagan *et al.* 1996) and to which light, water, and nutrient availability are integrated simultaneously with changes in ecosystem structure and composition (e.g., R. Waring and Running 1998). Obviously, conceptualizing the integration of the many thousands of species and other components in a given ecosystem is virtually impossible. However, some global-scale models distinguish the biota only at the community level, if at all. The degree to which individual species are distinguished influences the representation of the variety of interactions and feedbacks that influence ecosystem parameters (Naeem 1998, Polis 1991b, Reagan *et al.* 1996). Similarly, models based on a limited set of variables to predict a single type of output (e.g., carbon flux) may fail to account for effects of other variables (e.g., effects of limiting nutrients, such as nitrogen, on carbon flux) (R. Waring and Running 1998). More general models require simplifying assumptions to expand their application and may lose accuracy as a consequence.

After the conceptual organization of the model has been determined, interaction strengths are quantified (Figs. 11.14 and 11.15), based on available data, or subjected to sensitivity analysis to identify the range of values that represent observed interaction (e.g., Benke and Wallace 1997, Dambacher *et al.* 2002, de Ruiter *et al.* 1995, Parton *et al.* 1993, Rastetter *et al.* 1991, 1997, Running and Gower 1991). Direct and indirect interactions can be represented in transition matrix form. For example, see the following:

$$
\begin{array}{cccccccc}
 & N_1 & N_2 & N_3 & N_4 & . & . & N_i \\
N_1 & \alpha_{11} & \alpha_{21} & \alpha_{31} & \alpha_{41} & . & . & \alpha_{i1} \\
N_2 & \alpha_{12} & \alpha_{22} & \alpha_{32} & \alpha_{42} & . & . & \alpha_{i2} \\
N_3 & \alpha_{13} & \alpha_{23} & \alpha_{33} & \alpha_{43} & . & . & \alpha_{i3} \\
N_4 & \alpha_{14} & \alpha_{24} & \alpha_{34} & \alpha_{44} & . & . & \alpha_{i4} \\
. & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & . \\
N_j & \alpha_{1j} & \alpha_{2j} & \alpha_{3j} & \alpha_{4j} & . & . & \alpha_{ij}
\end{array}
$$

where N_j is the *j*th ecosystem component and α_{ij} is the relative effect (direct + indirect) of N_j on N_i. When $N_i = N_j$, α_{ij} represents intrinsic (intraspecific) effects on numbers or mass. Differential equations of the general form:

$$N_{i(t+1)} = N_{it} + \sum(\alpha_{ij}N_{jt}) \qquad (11.1)$$

are used to calculate the transitional states of each component as input conditions change. Note the application of this inclusive equation to equations for growth of individual populations and interacting species in Chapters 6 and 8. Components must be linked so that changes in the number, mass, or energy or nutrient content of one component have appropriate effects on the numbers, masses, or energy or nutrient contents of other components. Models focused on species emphasize fluxes of energy or matter through food webs. Models focused on energy or matter pools emphasize fluxes of energy and matter among pools but may include important species that affect flux rates.

Ecosystem models are sensitive to effects of indirect interactions. Nutrient availability and directions of fluxes indirectly affect all organisms. For example, a direct predator–prey interaction reduces prey abundance and directs energy and nutrients through that predator, thereby indirectly affecting resources available for other organisms, as well as interactions between that prey and its competitors, hosts, and other predators (see Chapter 8). Ultimately, indirect effects

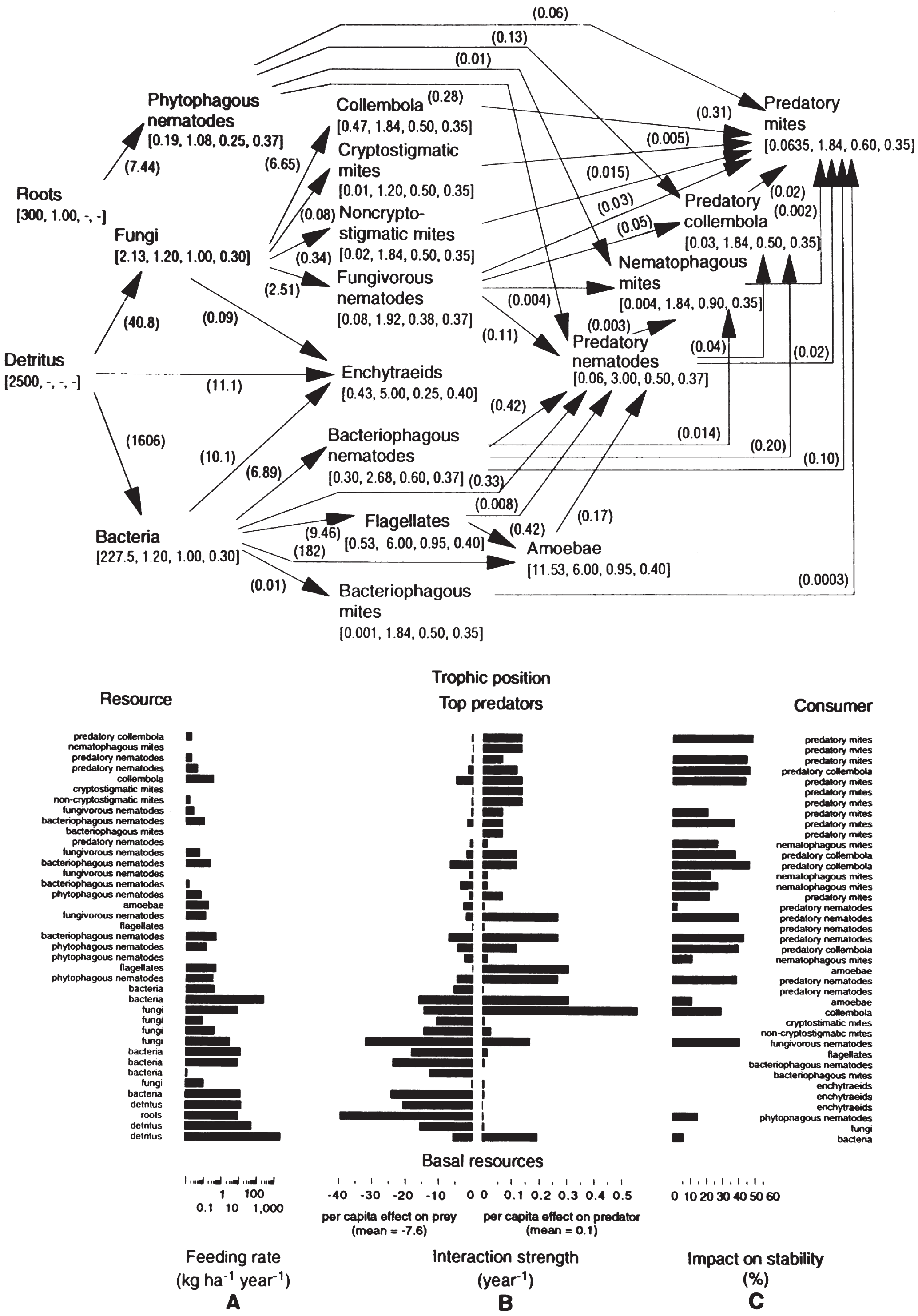


Fig. 11.14 Quantification of feeding rates (*top*), interaction strengths as per capita effects (*bottom*), and impact of these interactions on soil food web stability in conventional agriculture at Lovinkhoeve Experimental Farm, The Netherlands. From de Ruiter *et al.* (1995) with permission from the American Association for the Advancement of Science.

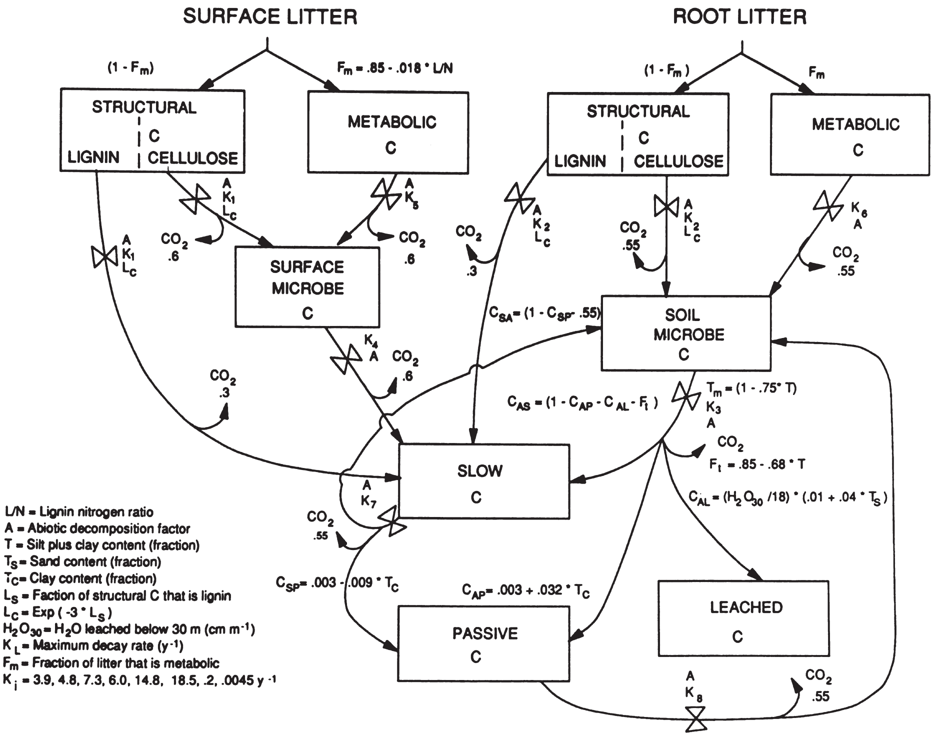


Fig. 11.15 Detail of carbon fluxes in the soil organic carbon submodel of the Century ecosystem model. This model can be coupled to the nitrogen submodel. From Parton *et al.* (1993) courtesy of the American Geophysical Union.

of this interaction can affect primary production, canopy cover, and resource availability in ways that determine climate, substrate, and resource conditions for the entire ecosystem. Nontrophic interactions are difficult to recognize and measure (Dambacher *et al.* 1999, 2002, O'Neill 2001); quantitative data are available for relatively few potential indirect interactions. Accordingly, the complexity of indirect, as well as direct, interactions is difficult to model but has important implications for how ecosystems respond to environmental changes (see Chapter 15).

A number of models have been developed to predict fluxes of energy or key elements, especially carbon or nitrogen, through ecosystems. However, as noted earlier in this chapter, interactions among various cycles (e.g., nitrogen and carbon cycles integrated through biomolecules, carbon and calcium cycles integrated in carbonates, or nitrogen and calcium cycles integrated through soil pH change) may confound predictions based on individual resources.

Comprehensive ecosystem models that integrate energy, carbon, water, and nutrient fluxes include FOREST-BGC/BIOME-BGC (Running and Gower 1991) and CENTURY (e.g., Fig. 11.15; Parton *et al.* 1993), which have been modified to represent a variety of ecosystem types. These models are useful for predicting global biogeochemical processes because they integrate common ecosystem processes in a logical framework; have minimum requirements for detail of inputs for ecosystem characteristics; and account for the mass balances of multiple nutrients moving through interacting plants, detritus, decomposers, and abiotic pools. This ecological stoichiometry (Daufresne and Loreau 2001, Sterner and Elser 2002) provides a tool for evaluating consequences of changes in mass balances among multiple elements as a result of changes in environmental conditions or community interactions. The effects of insects and other invertebrates have been incorporated poorly, or not at all, in these, or other, existing ecosystem models. At best, insects usually are combined as "insects" or "arthropods," thereby losing valuable information about this diverse group, species of which can respond dramatically and differentially to environmental change and have major effects on ecosystem properties (Chapters 12–14).

VI. SUMMARY

An ecosystem represents the integration of the biotic community and the abiotic environment. The capacity of the community to modify its environment depends on its structure and the degree to which it controls energy flow, biogeochemical cycling, and climatic conditions.

Ecosystem structure reflects the organization of various abiotic and biotic pools that exchange energy and matter. Abiotic pools are the atmosphere, oceans, and sediments that represent the sources of energy and matter for biotic use. Biotic pools are the various organisms (individuals, species populations, functional groups, or trophic levels) in the community. Autotrophs (or primary producers) are those organisms that can acquire resources from abiotic pools. Heterotrophs (or secondary producers) are those organisms that must acquire their resources from other organisms. Energy and matter storage in these pools can be represented as pyramids of productivity, numbers, or biomass.

Energy available to ecosystems comes primarily from solar radiation, captured and stored in carbohydrates by primary producers (autotrophs) through the process of photosynthesis. The total rate at which energy is captured (GPP) depends on exposure to sunlight, availability of water, and biomass. Some of the energy from gross primary production is expended through plant respiration. The remaining net primary production is stored as plant biomass and is the source of energy and matter for heterotrophs. Primary heterotrophs (herbivores) feed on autotrophs, whereas secondary heterotrophs (predators) feed on other heterotrophs. Consumption transfers the energy stored in consumed biomass to the higher trophic level, with some lost as egestion and consumer respiration. Generally, <10% of the energy available at each trophic level is converted into biomass at the next higher trophic level, although predators generally have a higher efficiency of conversion than do herbivores. Energy remaining in organisms at the time of death becomes available to decomposers that release the remaining energy through respiration.

Energy is the currency with which organisms acquire and concentrate material resources necessary for growth and reproduction. Material resources are often available in limited supply, favoring mechanisms that facilitate retention and reuse within the ecosystem. Biogeochemical cycling represents the processes whereby material resources, including water, carbon, nitrogen, and mineral elements, are acquired from abiotic pools and recycled among trophic levels, with eventual return to abiotic pools. The efficiency with which these materials are recycled and conserved, rather than lost to abiotic pools, buffers an ecosystem against resource depletion and reduced productivity. Hence, ecosystems become organized in ways that maximize the capture and storage of resources among organisms. Resources egested or excreted during trophic transfers, as well as dead organisms, become available to decomposers that rapidly acquire and store the nutrients from organic matter. Nutrients released by decomposers become available for exchange among soil and aquatic organisms and for plant uptake. Microorganisms are particularly instrumental in making nitrogen available for plant uptake, with different specialists fixing atmospheric nitrogen as ammonia and converting ammonia to nitrate and organic nitrogen to ammonia. Volatilization by fire and denitrification by anaerobic bacteria complete the cycle by returning elemental nitrogen to the atmosphere.

Ecosystems also modify local and regional climatic conditions. The degree to which vegetation reduces soil warming, evaporation, erosion, and wind speed depends on density and vertical architecture. Insects and other organisms affect vegetation structure and hence canopy–atmosphere interactions. Tall, multicanopied forests are most effective at modifying surface temperatures, relative humidities, and wind speed, thereby ameliorating local and regional fluctuations in temperature, wind speed, and precipitation.

Models have become important tools for synthesizing complex, and often incomplete, data for prediction of ecosystem responses to, and effects on, global environmental changes. Ecosystem models differ in structure and degree of simplification. Effects of insects on a variety of ecosystem parameters have been largely ignored in ecosystem models.

12

Herbivory

HERBIVORY IS THE RATE OF CONSUMPTION BY ANIMALS OF ANY PLANT parts, including foliage, stems, roots, flowers, fruits, or seeds. Direct effects of insects on plant reproductive parts are addressed in Chapter 13. Herbivory is a key ecosystem process that reduces density of plants or plant materials, transfers mass and nutrients to the soil or water column, and affects habitat and resource conditions for other organisms. Insects are the primary herbivores in many ecosystems, and their effect on primary production can equal or exceed that of more conspicuous vertebrate grazers in grasslands (e.g., A. Andersen and Lonsdale 1990, Gandar 1982, Sinclair 1975, Weisser and Siemann 2004, Wiegert and Evans 1967).

Loss of plant material through herbivory generally is negligible, or at least inconspicuous, but periodic outbreaks of herbivores have a well-known capacity to reduce growth and survival of host species by as much as 100% and to alter vegetation structure over large areas. A key aspect of herbivory is its variation in intensity among plant species, reflecting biochemical interactions between the herbivore and the various host and nonhost species that comprise the vegetation (see Chapter 3).

Effects of herbivory on ecosystem processes depend on the type of herbivore and pattern of consumption, as well as its intensity. Measurement and comparison of herbivory and its effects among ecosystems and environmental conditions remain problematic as a result of lack of standardized techniques for measuring or manipulating intensity. Few studies have assessed the effects of herbivory on ecosystem processes other than primary production. Nevertheless, accumulating evidence indicates that effects of herbivory on ecosystem processes, including primary production, are complex. Ecosystem management practices that exacerbate or suppress herbivory may be counterproductive.

I. TYPES AND PATTERNS OF HERBIVORY

A. Herbivore Functional Groups

Herbivorous insects that have similar means of exploiting plant parts for food can be classified into feeding guilds or functional groups. Groups of plant-feeders include *chewers* that consume foliage, stems, flowers, pollen, seeds, and roots; *miners* and *borers* that feed between plant surfaces; *gall-formers* that reside and feed within the plant and induce the production of abnormal growth reactions by plant tissues; *sap-suckers* that siphon plant fluids; and *seed predators* and *frugivores* that consume the reproductive parts of plants (Romoser and Stoffalano 1998). Some species, such as seed predators, seedling-eaters, and tree-killing bark beetles, are true plant predators, but most herbivores function as plant parasites because they normally do not kill their hosts, but instead feed on the living plant without causing death (Price 1980). These different modes of consumption affect plants in different ways. For example, *folivores* (species that chew foliage) directly reduce the area of photosynthetic tissue, whereas sap-sucking insects affect the flow of fluids and nutrients within the plant and *root-feeders* reduce plant capacity to acquire nutrients or remain upright.

Folivory is the best-studied aspect of herbivory. In fact, the term herbivory often is used even when folivory alone is measured because loss of foliage is the most obvious and easily quantified aspect of herbivory. The loss of leaf area can be used to indicate the effect of herbivory. In contrast, other herbivores such as sap-suckers or root-borers cause less conspicuous losses that are more difficult to measure. Nonetheless, Schowalter *et al.* (1981c) reported that calculated loss of photosynthates to sap-suckers greatly exceeded measured foliage loss to folivores in an early successional deciduous forest. Sap-suckers and root-feeders also may have long-term effects (e.g., through disease transmission or altered rates of nutrient acquisition or growth) (J.P. Smith and Schowalter 2001).

B. Measurement of Herbivory

Effects of herbivory on ecosystem processes are determined by temporal and spatial variability in the magnitude of consumption. Clearly, evaluation of the effects of herbivory requires robust methods for measuring herbivory as well as primary productivity and other ecosystem processes. Measurement of herbivory can be difficult, especially for underground plant parts and forest canopies, and has not been standardized. Several methods commonly used to measure herbivory have been compared by Filip *et al.* (1995), Landsberg (1989), and Lowman (1984).

The simplest and most widely used technique is the measurement of feeding rate by individual herbivores and extrapolation to feeding rate by a population. This technique provides relatively accurate rates of consumption and can be used to estimate per capita feeding rate for sap-suckers as well as folivores (e.g., Gandar 1982, Schowalter *et al.* 1981c, B. Stadler and Müller 1996). Insect folivores usually consume 50–150% of their dry body mass per day (Blumer and

Diemer 1996, Reichle and Crossley 1967, Reichle *et al.* 1973, Schowalter *et al.* 1981c).

Rates of sap and root consumption are difficult to measure, but a few studies have provided limited information. For example, honeydew production by individual sap-sucking insects can be used as an estimate of their consumption rates. Stadler and Müller (1996) and Stadler *et al.* (1998) reported that individual spruce aphids, *Cinara* spp., produced from 0.1 mg honeydew day^{-1} for first instars to 1 mg day^{-1} for adults, depending on aphid species, season, and nutritional status of the host. Schowalter *et al.* (1981c) compiled consumption data from studies of eight herb- and tree-feeding aphids (Auclair 1958, 1959, 1965, Banks and Macaulay 1964, Banks and Nixon 1959, M. Day and Irzykiewicz 1953, Llewellyn 1972, Mittler 1958, 1970, Mittler and Sylvester 1961, Van Hook *et al.* 1980, M. Watson and Nixon 1953), a leafhopper (M. Day and McKinnon 1951), and a spittlebug (Wiegert 1964) that yielded an average consumption rate of 2.5 mg dry sap mg^{-1} dry insect day^{-1}.

Several factors affect the rate of sap consumption. P. Andersen *et al.* (1992) found that leafhopper feeding rate was related to xylem chemistry and fluid tension. Feeding rates generally increased with amino-acid concentrations and decreased with xylem tension, ceasing above tensions of 2.1 Mpa when plants were water stressed. Stadler and Müller (1996) reported that aphids feeding on poor-quality hosts with yellowing needles produced twice the amount of honeydew as did aphids feeding on high-quality hosts during shoot expansion, but this difference disappeared by the end of shoot expansion. Banks and Nixon (1958) reported that aphids tended by ants approximately doubled their rates of ingestion and egestion.

Measurement of individual consumption rate has limited utility for extrapolation to effects on plant growth because more plant material may be lost, or not produced, than actually consumed as a consequence of wasteful feeding or mortality to meristems (e.g., Blumer and Diemer 1996, Gandar 1982). For example, Schowalter (1989) reported that feeding on Douglas-fir, *Pseudotsuga menziesii,* buds by a bud moth, *Zeiraphera hesperiana,* caused an overall loss of <1% of foliage standing crop, but the resulting bud mortality caused a 13% reduction in production of shoots and new foliage.

Herbivory can be estimated as the amount of frass collected per unit time (Fig. 12.1), adjusted for assimilation efficiency (Chapter 4). This measure is sensitive to conditions that affect frass collection, such as precipitation. Hence, frass generally must be collected prior to rainfall events. Mizutani and Hijii (2001) measured the effect of precipitation on frass collection in conifer and deciduous broad-leaved forests in central Japan and calculated correction factors for loss of frass as a result of precipitation. Such methods enhance the use of frass collection for estimation of herbivory.

Percentage leaf area missing can be measured at discrete times throughout the growing season. This percentage can be estimated visually but is sensitive to observer bias (Landsberg 1989). Alternatively, leaf area of foliage samples is measured, then remeasured after holes and missing edges have been reconstructed (e.g., Filip *et al.* 1995, H. Odum and Ruiz-Reyes 1970, Reichle *et al.* 1973,

FIG. 12.1 Insect herbivore feces collected on understory vegetation in cypress-tupelo swamp in southern Louisiana, United States.

Schowalter *et al.* 1981c). Reconstruction originally was accomplished using tape or paper cutouts. More recently, computer software has become available to reconstruct leaf outlines and fill in missing portions (Hargrove 1988). Neither method accounts for expansion of holes as leaves expand, for compensatory growth (to replace lost tissues), for completely consumed or prematurely abscissed foliage, for foliage loss as a result of high winds, nor for herbivory by sap-suckers (Faeth *et al.* 1981, Hargrove 1988, Lowman, 1984; Reichle *et al.* 1973, Risley and Crossley, 1993, Stiling *et al.* 1991).

The most accurate method for measuring loss to folivores is detailed life table analysis of marked leaves at different stages of plant growth (Aide 1993, Filip *et al.* 1995, Hargrove 1988, Lowman 1984). Continual monitoring permits accounting for consumption at different stages of plant development, with consequent differences in degree of hole expansion, compensatory growth, and complete consumption or loss of damaged leaves (Lowman 1984, Risley and Crossley 1993). Estimates of herbivory based on long-term monitoring often are 3–5 times the estimates based on discrete measurement of leaf area loss (Lowman 1984, 1995). Filip *et al.* (1995) compared continual and discrete measurements of herbivory for 12 tree species in a tropical deciduous forest in Mexico. Continual measurement provided estimates 1–5 times higher than those based on discrete sampling. On average, measurements from the two techniques differed by a factor of 2. Broad-leaved plants are more amenable to this technique than are needle-leaved plants.

Several methods also have been used to measure effects of herbivory on plants or ecosystem processes. A vast literature is available on the effects of herbivory on growth of individual plants or plant populations (e.g., Crawley 1983, Huntly 1991). However, most studies have focused on effects of above-ground herbivores on above-ground plant parts. Few studies have addressed root-feeding insects or root responses to herbivory (M. Hunter 2001a, Morón-Ríos *et al.* 1997b, J. Smith and Schowalter 2001, D. Strong *et al.* 1995). J. Smith and Schowalter (2001) and D. Strong *et al.* (1995) found that roots can take at least a year to recover from herbivory, indicating that short-term experiments may be inadequate to estimate the herbivore effects on roots.

At the ecosystem level, a number of studies have compared ecosystem processes between sites naturally infested or not infested during population irruptions. Such comparison confounds herbivore effects with environmental gradients that may be responsible for the discontinuous pattern of herbivory (Chapter 7). Hurlbert (1984) discussed the importance of independent, geographically intermixed replicate plots for comparison of treatment effects. This requires manipulation of herbivore abundances in replicate plots to evaluate effects on ecosystem parameters.

A few studies have involved experimental manipulation of herbivore numbers, especially on short vegetation (e.g., Kimmins 1972, McNaughton 1979, Morón-Ríos *et al.* 1997a, Schowalter *et al.* 1991, Seastedt 1985, Seastedt *et al.* 1983, S. Williamson *et al.* 1989), but this technique clearly is difficult in mature forests. The most common method has been comparison of ecosystem processes in plots with nominal herbivory versus chemically suppressed herbivory (e.g., V.K. Brown *et al.* 1987, 1988, D. Gibson *et al.* 1990, Louda and Rodman 1996, Seastedt *et al.* 1983). However, insecticides can provide a source of limiting nutrients that may affect plant growth. Carbaryl, for example, contains nitrogen, which is frequently limiting and likely to stimulate plant growth. Manipulation of herbivore abundance is the best means for relating effects of herbivory over a range of intensity (e.g., Schowalter *et al.* 1991, S. Williamson *et al.* 1989), but such manipulation of herbivore abundance often is difficult (Baldwin 1990, Crawley 1983, Schowalter *et al.* 1991). Cages constructed of fencing or mesh screening are used to exclude or contain experimental densities of herbivores (e.g., McNaughton 1985, Palmisano and Fox 1997). Mesh screening should be installed in a manner that does not restrict air movement or precipitation and thereby alter growing conditions within the cage.

A third option has been to simulate herbivory by clipping or pruning plants or by punching holes in leaves (e.g., Honkanen *et al.* 1994). This method avoids the problems of manipulating herbivore abundance but may fail to represent important aspects of herbivory, other than physical damage, that influence its effects (e.g., Baldwin 1990, Crawley 1983, Frost and Hunter 2005, Lyytikäinen-Saarenmaa 1999). For example, herbivore saliva may stimulate growth of some plant species (M. Dyer *et al.* 1995), and natural patterns of consumption and excretion affect litter condition, decomposition, and nutrient supply (Frost and Hunter 2005, Hik and Jefferies 1990, Lovett and Ruesink 1995, B. Stadler *et al.* 1998, Zlotin and Khodashova 1980). Lyytikäinen-Saarenmaa (1999) reported that artificial defoliation of Scots pine, *Pinus sylvestris,* saplings caused greater growth reduction than did comparable herbivory by sawflies, *Diprion pini* and *Neodiprion sertifer,* in May and June, whereas the opposite trend was seen for trees subjected to treatments in July and August.

The choice of technique for measuring herbivory and its effects depends on several considerations. The method of measurement must be accurate, efficient, and consistent with objectives. Measurement of percentage leaf area missing at a point in time is an appropriate measure of the effect of herbivory on canopy porosity, photosynthetic capacity, and canopy–soil or canopy–atmosphere interactions but does not represent the rate of consumption or removal of plant material. Access to some plant parts is difficult, precluding continuous monitoring. Hence, limited data are available for herbivory on roots or in forest canopies. Simulating herbivory by removing plant parts or punching holes in leaves fails to represent some important effects of herbivory, such as salivary toxins or stimulants or flux of canopy material to litter as feces, but it does overcome the difficulty of manipulating abundances of herbivore species.

Similarly, the choice of response variables depends on objectives. Most studies have examined only effects of herbivory on above-ground primary production, consistent with emphasis on foliage and fruit production. However, herbivores feeding above ground also affect root production and rhizosphere processes (Gehring and Whitham 1991, 1995, Holland *et al.* 1996, Rodgers *et al.* 1995, J. Smith and Schowalter 2001). Effects on some fluxes, such as dissolved organic carbon in honeydew, are difficult to measure (B. Stadler *et al.* 1998). Some effects, such as compensatory growth and altered community structure, may not become apparent for long time periods following herbivore outbreaks (Alfaro and Shepherd 1991, Wickman 1980).

C. Spatial and Temporal Patterns of Herbivory

All plant species support characteristic assemblages of insect herbivores, although some plants host a greater diversity of herbivores and exhibit higher levels of herbivory than do others (e.g., Coley and Aide 1991, de la Cruz and Dirzo 1987). Some plants tolerate continuous high levels of herbivory, whereas other species show negligible loss of plant material (Carpenter and Kitchell 1984, Lowman and Heatwole 1992, McNaughton 1979, Schowalter and Ganio 2003), and some plant species suffer mortality at lower levels of herbivory than do others. Herbivory usually is concentrated on the most nutritious or least defended plants and plant parts (Chapter 3; Aide and Zimmerman 1990).

The consequences of herbivory vary significantly, not just among plant–herbivore interactions but also as a result of different spatial and temporal factors (Huntly 1991, Maschinski and Whitham 1989). For example, water or nutrient limitation and ecosystem fragmentation can affect significantly the ability of the host plant to respond to herbivory (e.g., Chapin *et al.* 1987, Kolb *et al.* 1999, Maschinski and Whitham 1989, W. Webb 1978). The timing of herbivory with respect to plant development and the intervals between attacks also have important effects on ecosystem processes (Hik and Jefferies 1990).

Herbivory usually is expressed as daily or annual rates of consumption and ranges from negligible to several times the standing crop biomass of foliage (Table 12.1), depending on ecosystem type, environmental conditions, and regrowth capacity of the vegetation (Lowman 1995, Schowalter and Lowman 1999). Herbivory for particular plant species can be integrated at the ecosystem level by weighting rates for each plant species by its biomass or leaf area. When the preferred hosts are dominant plant species, loss of plant parts can be dramatic and conspicuous, especially if these species are slow to replace lost parts (B. Brown and Ewel 1987). For example, defoliation of evergreen forests may be visible for months, whereas deciduous forests and grasslands are adapted for periodic replacement of foliage and usually replace lost foliage quickly. Eucalypt forests are characterized by chronically high rates of herbivory (Fox and Morrow 1992). Some species lose more than 300% of their foliage standing crop annually, based on life table studies of marked leaves (Lowman and Heatwole 1992).

Comparison of herbivory among ecosystem types (see Table 12.1) indicates considerable variation. The studies in Table 12.1 reflect the range of measurement techniques described earlier in this chapter. Most are short-term snapshots of folivory, often for only a few plant species; do not provide information on herbivory by sap-suckers or root feeders; and do not address any deviation in environmental conditions, plant chemistry, or herbivore densities from long-term means during the period of study. Long-term studies using standardized techniques are necessary for meaningful comparison of herbivory rates.

Cebrián and Duarte (1994) compiled data from a number of aquatic and terrestrial ecosystems and found a significant relationship between percentage plant material consumed by herbivores and the rate of primary production. Herbivory ranged from negligible to >50% of photosynthetic biomass removed daily. Rates were greatest in some phytoplankton communities where herbivores consumed all production daily and least in some forests where herbivores removed <1% of production. Insects are the primary herbivores in forest ecosystems (Janzen 1981, Wiegert and Evans 1967) and account for 11–73% of total herbivory in grasslands, where native vertebrate herbivores remove an additional 15–33% of production (Detling 1987, Gandar 1982, Sinclair 1975). Temperate deciduous forests and tropical evergreen forests show similar annual losses of 3–20%, based on discrete sampling of leaf area loss (Coley and Aide 1991, Landsberg and Ohmart 1989, H. Odum and Ruiz-Reyes 1970, Schowalter and Ganio 1999, Schowalter *et al.* 1986, Van Bael *et al.* 2004). Aquatic ecosystems, evergreen forests, and grasslands, which replace lost photosynthetic tissue continuously, often lose several times their standing crop biomass to herbivores annually, based on loss of marked foliage or on herbivore exclusion (Carpenter and Kitchell 1984, Cebrián and Duarte 1994, Crawley 1983, Landsberg 1989, Lowman and Heatwole 1992, McNaughton 1979).

In addition to the conspicuous loss of photosynthetic tissues, terrestrial plants lose additional material to sap-suckers and root feeders. Schowalter *et al.* (1981c) compiled data on rates of sap consumption to estimate turnover of 5–23% of foliage standing crop biomass through sap-sucking herbivores, in addition to 1–2% turnover through folivores in a temperate deciduous forest. J. Smith and

TABLE 12.1 Herbivory measured in temperate and tropical ecosystems (including understory). Expanded from Lowman (1995).

Location	Ecosystem type	Level of grazing	Technique[a]	Source
Tropical				
Costa Rica	Tropical forest	7.5% (new leaves)	1	N. Stanton (1975)
	Tropical evergreen forest	30% (old)	1	N. Stanton (1975)
Panama	Tropical evergreen forest	13%	1	Wint (1983)
Panama (BCI)	Tropical evergreen forest	8% (6% insect; 1–2% vertebrates)	1, 2	Leigh and Smythe (1978)
		15%	1, 2	Leigh and Windsor (1982)
	Understory only	21% (but up to 190%)	3	Coley (1983)
Puerto Rico	Tropical evergreen forest	7.8%	1	H. Odum and Ruiz-Reyes (1970)
		5.5–16.1%	1	Benedict (1976)
		2–6%	1	Schowalter (1994a)
		2–13%	1	Schowalter and Ganio (1999)
Mexico	Tropical deciduous forest	7–9%	1	Filip *et al.* (1995)
	Tropical deciduous forest	17%	3	Filip *et al.* (1995)
Venezuela	Understory only	0.1–2.2%	1	Golley (1977)
New Guinea	Tropical evergreen forest	9–12%	1	Wint (1983)
Australia	Montane or cloud forest	26%	3	Lowman (1984)
	Warm temperate forest	22%	3	Lowman (1984)
	Subtropical forest	14.6%	3	Lowman (1984)
Cameroon	Tropical evergreen forest	8–12%	3	Lowman *et al.* (1993)

Tanzania	Tropical grassland	14–38% (4–8% insect; 8–34% vertebrates)	4	Sinclair (1975)
South Africa	Tropical savanna	38% (14% insect; 24% vertebrates)	4	Gandar (1982)
Temperate				
North America	Deciduous forest	2–10%	1	Reichle *et al.* (1973)
		1–5%	1	Schowalter *et al.* (1981c)
	Herbaceous sere	3%	4	Crossley and Howden (1966)
	Coniferous forest	<1%	1	Schowalter (1989)
		1–6%	1	Schowalter (1995)
	Grassland	5–15%	1	Detling (1987)
Australia	Evergreen forest	15–300%	3	Lowman and Heatwole (1992)
	Dry forest	5–44%	1	Fox and Morrow (1983)
		3–6%	2	Ohmart *et al.* (1983)
Europe	Deciduous forest	7–10%	1	Nielsen (1978)
	Alpine grassland	19–30%	1	Blumer and Diemer (1996)

[a] 1, Leaf area missing; 2, litter or frass collection; 3, turnover of marked foliage; 4, individual consumption rates. Please see extended permission list pg 572.

Schowalter (2001) found that shoot-feeding aphids, *Cinara pseudotsugae,* significantly reduced Douglas-fir root tissue density and growth and that at least 1 year was required for recovery after feeding ceased. V.K. Brown and Gange (1991) and Morón-Ríos *et al.* (1997a) reported that root-feeding insects can reduce primary production of grasses by 30–50%.

Factors that promote herbivore population growth (e.g., abundant and susceptible hosts) also increase herbivory (see Chapters 6 and 8). Proportional losses of foliage to folivores generally are higher in less diverse ecosystems, compared to more diverse ecosystems (Kareiva 1983), but the intensity of herbivory also depends on the particular species composition of the vegetation (R. Moore and Francis 1991, R. Moore *et al.* 1991). B. Brown and Ewel (1987) demonstrated that ecosystem-level foliage losses per unit ground area were similar among four tropical ecosystems that varied in vegetation diversity, but the proportional loss of foliage standing crop was highest in the less diverse ecosystems. Nevertheless, rare plant species in diverse ecosystems can suffer intense herbivory, especially under conditions that increase their apparency or acceptability (Brown and Ewel 1987, Schowalter and Ganio 1999). C. Fonseca (1994) reported that an Amazonian myrmecophytic canopy tree showed 10-fold greater foliage losses when ants were experimentally removed than when ants were present.

Seasonal and annual changes in herbivore abundance affect patterns and rates of herbivory, but the relationship may not be linear, depending on variation in per capita rates of consumption or wasteful feeding with increasing population density (Crawley 1983, B. Stadler *et al.* 1998). Herbivory in temperate forests usually is concentrated in the spring during leaf expansion (Feeny 1970, M. Hunter 1987). M. Hunter (1992) reported that more than 95% of total defoliation on *Quercus robur* in Europe occurs between budburst in April and the beginning of June. Although some herbivorous insects prefer mature foliage (Cates 1980, Sandlin and Willig 1993, Volney *et al.* 1983), most defoliation events are associated with young foliage (Coley 1980, M. Hunter 1992, R. Jackson *et al.* 1999, Lowman 1985). Herbivory also is highly seasonal in tropical ecosystems. Tropical plants produce new foliage over a more protracted period than do temperate plants, but many produce new foliage in response to seasonal variation in precipitation (Aide 1992, Coley and Aide 1991, Lowman 1992, Ribeiro *et al.* 1994). Young foliage may be grazed more extensively than older foliage in tropical rainforests (Coley and Aide 1991, Lowman 1984, 1992). Schowalter and Ganio (1999) reported significantly greater rates of leaf area loss during the "wet" season than during the "dry" season in a tropical rainforest in Puerto Rico (Fig. 12.2). However, seasonal peaks of leaf expansion and herbivory are broader in tropical ecosystems than in temperate ecosystems.

Few studies have addressed long-term changes in herbivore abundances or herbivory as a result of environmental changes (see Chapter 6). However, disturbances often induce elevated rates of herbivory at a site. Periods of elevated herbivory frequently are associated with drought (Mattson and Haack 1987; Chapter 6). Although herbivore outbreaks are usually associated with temperate forests, Van Bael *et al.* (2004) documented a general outbreak by several lepidopteran species on multiple tree and liana species during an El Niño–induced

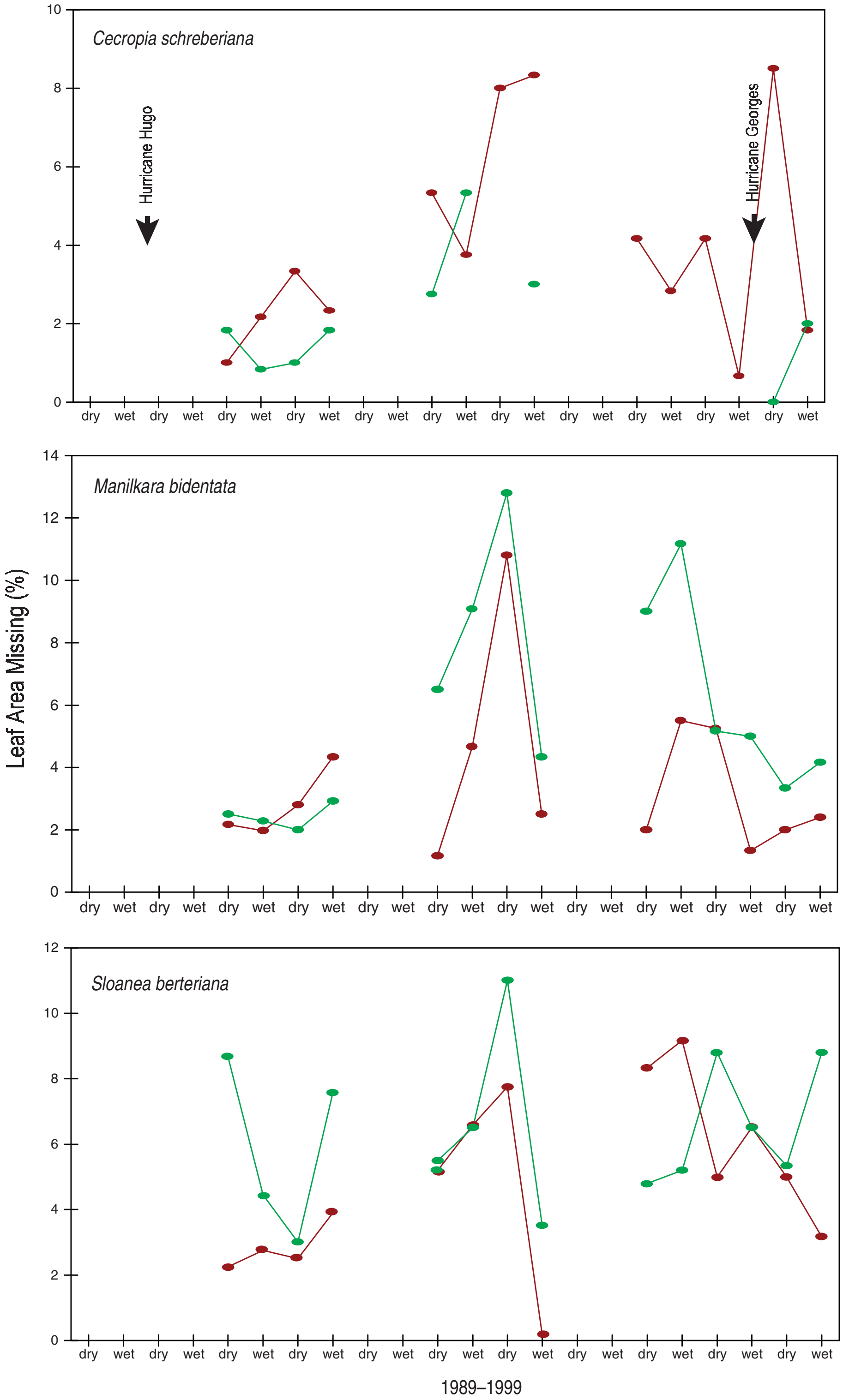


FIG. 12.2 Effects of tree species, hurricane disturbance, and seasonal cycles on leaf area missing in a tropical rainforest in Puerto Rico, as affected by two hurricanes (1989 and 1998) and a drought (1994–1995). *Cecropia* is an early successional tree; *Manilkara* and *Sloanea* are late successional trees. Green lines represent intact forest (lightly disturbed); red lines represent treefall gaps.

drought in Panama. Torres (1992) reported outbreaks of several lepidopteran species on understory forbs and vines following Hurricane Hugo in Puerto Rico. These studies suggest that outbreaks may be common but less conspicuous in tropical forests. Other disturbances that injure plants also may increase herbivory, especially by root feeders and stem borers (e.g., T. Paine and Baker 1993, Witcosky *et al.* 1986).

Changes in vegetation associated with disturbance or recovery affect temporal patterns of herbivory. Bach (1990) reported that intensity of herbivory declined during succession in dune vegetation in Michigan (Fig. 12.3). Coley (1980, 1982, 1983), Coley and Aide (1991), and Lowman and Box (1983) found that rapidly growing early successional tree species showed higher rates of herbivory than did slow-growing late successional trees. Schowalter (1995), Schowalter and Ganio (1999, 2003), and Schowalter and Crossley (1988) compared canopy herbivore abundances and folivory in replicated disturbed (harvest or hurricane) and undisturbed patches of temperate deciduous, temperate coniferous, and tropical evergreen forests. In all three forest types, disturbance resulted in greatly increased abundances of sap-suckers and somewhat increased abundances of folivores on abundant, rapidly growing early successional plant species. The resulting shift in biomass dominance from folivores to sap-suckers following disturbance resulted in an elevated flux of primary production as soluble photosynthates, relative to fragmented foliage and feces. Schowalter *et al.* (1981c) calculated that loss of photosynthate to sap-suckers increased from 5% of foliage standing crop in undisturbed forest to 20–23% of foliage standing crop during the first 2 years following clearcutting, compared to relatively consistent losses of 1–2% to folivores. Torres (1992) reported a sequence of defoliator outbreaks on early successional herbs and shrubs during several months following Hurricane Hugo in Puerto Rico. As each plant species became dominant at a site, severe defoliation facilitated its replacement by other plant species. Continued measurement of herbivory over long time periods will be necessary to relate changes in the intensity of herbivory to environmental changes and to effects on ecosystem processes.

II. EFFECTS OF HERBIVORY

Herbivory affects a variety of ecosystem properties, primarily through differential changes in survival, productivity, and growth form among plant species. Herbivory is not evenly distributed among plant species or over time. Rather, some species are subject to greater herbivory than are others, and relative herbivory among plant species varies with environmental conditions (e.g., Coley 1980, Coley and Aide 1991, Crawley 1983, Schowalter and Ganio 1999). These differential effects on host conditions alter vegetation structure, energy flow, and biogeochemical cycling and often predispose the ecosystem to characteristic disturbances.

The observed severity of herbivore effects in agroecosystems and some native ecosystems has led to a widespread perception of herbivory as a disturbance (see Chapter 2). This perception raises a number of issues. How can a normal trophic

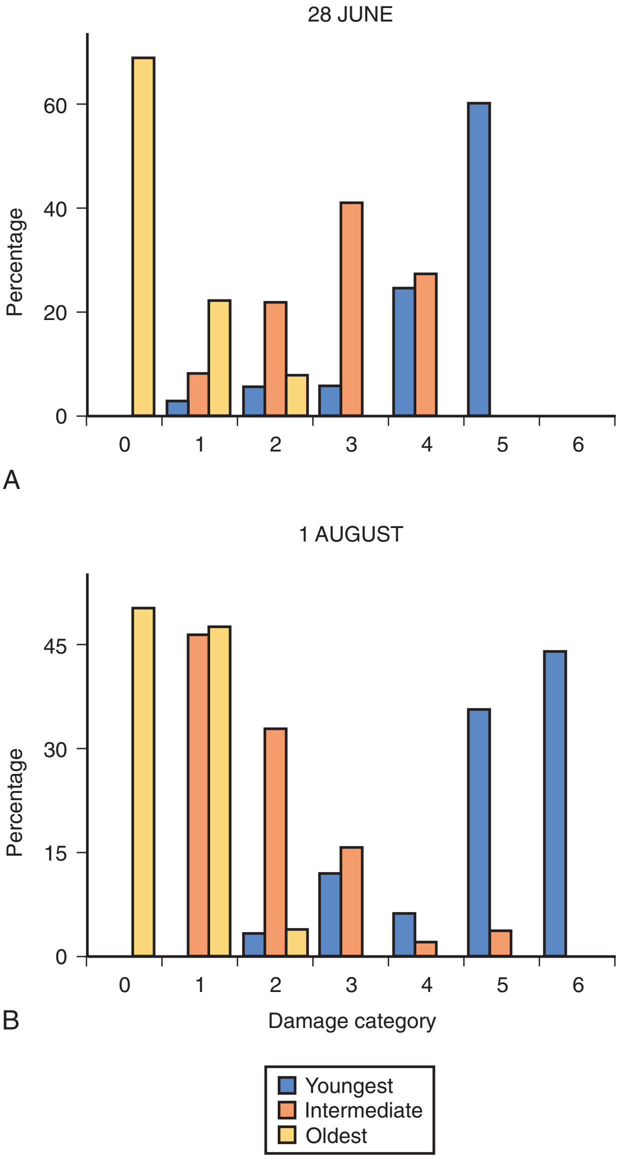


FIG. 12.3 Herbivore damage to plants in young, intermediate, and old successional sites in sand dune vegetation in Michigan in June (*A*) and August (*B*) 1988. Percentages are averages for leaves on upper and lower canopy branches by damage category: 0, 0% damage; 1, 1–5%; 2, 6–25%; 3, 26–50%; 4, 51–75%; 5, 76–100%; and 6, no leaves remaining. From Bach (1990) with permission from the Ecological Society of America.

process also be a disturbance? Is predation a disturbance? At what level does herbivory become a disturbance? Do the normally low levels of 5–20% loss of net primary productivity (NPP) constitute disturbance? Although debate may continue over whether herbivory is a disturbance (Veblen *et al.* 1994, P. White and Pickett 1985) rather than simply an ecosystem process

(Schowalter 1985, Schowalter and Lowman 1999, Willig and McGinley 1999), herbivory can dramatically alter ecosystem structure and function over large areas.

A. Plant Productivity, Survival, and Growth Form

Traditionally, herbivory has been viewed solely as a process that reduces primary production. As described in the preceding text, herbivory can remove several times the standing crop of foliage, alter plant growth form, or kill all plants of selected species over large areas during severe outbreaks. However, several studies indicate more complex effects of herbivory. The degree to which herbivory affects plant survival, productivity, and growth form depends on the plant parts affected; plant condition, including the stage of plant development; and the intensity of herbivory.

Different herbivore species and functional groups (e.g., folivores, sap-suckers, shoot borers, and root feeders) determine which plant parts are affected. Folivores and leaf miners reduce foliage surface area and photosynthetic capacity, thereby limiting plant ability to produce and accumulate photosynthates for growth and maintenance. In addition to direct consumption of foliage, much unconsumed foliage is lost as a result of wasteful feeding by folivores (Risley and Crossley 1993) and induction of leaf abscission by leaf miners (Faeth *et al.* 1981, Stiling *et al.* 1991). Sap-suckers and gall-formers siphon fluids from the plant's vascular system and reduce plant ability to accumulate nutrients or photosynthates for growth and maintenance. Shoot borers and bud feeders damage meristems and growing shoots, altering plant growth rate and form. Root feeders reduce plant ability to acquire water and nutrients. Reduced accumulation of energy often reduces flowering or seed production, often completely precluding reproduction (V.K. Brown *et al.* 1987, Crawley 1989). For example, M. Parker (1985) and Wisdom *et al.* (1989) reported that flower production by composite shrubs, *Gutierrezia microcephala,* was reduced as much as 80% as a consequence of grazing by the grasshopper, *Hesperotettix viridis.* Many sap-suckers and shoot- and root-feeders also transmit or facilitate growth of plant pathogens, including viruses, bacteria, fungi, and nematodes (e.g., C. Jones 1984). Alternatively, folivory may induce resistance to subsequent infection by plant pathogens (Hatcher *et al.* 1995).

Plant condition is affected by developmental stage and environmental conditions and determines herbivore population dynamics (see Chapters 3 and 6) and plant capacity to compensate for herbivory. Low or moderate levels of herbivory often increase photosynthesis and stimulate plant productivity (e.g., Belovsky and Slade 2000, Carpenter and Kitchell 1984, Carpenter *et al.* 1985, C. Carroll and Hoffman 1980, Detling 1987, 1988, M. Dyer *et al.* 1993, Kolb *et al.* 1999, Lowman 1982, McNaughton 1979, 1993a, Pedigo *et al.* 1986, Trumble *et al.* 1993, S. Williamson *et al.* 1989), whereas severe herbivory usually results in mortality or decreased fitness (Detling 1987, 1988, Marquis 1984, S. Williamson *et al.* 1989). Healthy plants can replace lost foliage, resulting in higher annual primary production, although standing crop biomass of plants usually is reduced.

Kolb *et al.* (1999) experimentally evaluated a number of factors that potentially influence the effect of western spruce budworm, *Choristoneura occidentalis,* defoliation on potted Douglas-fir seedling physiology and growth. They demonstrated that seedling biomass decreased, but photosynthetic rate; stomatal conductance; foliar concentrations of N, Ca, and Mg; and soil water potential increased with increasing intensity of herbivory. Increased photosynthesis and reduced water stress may improve tree survival in environments where water stress has a more serious negative effect on survival than does defoliation. Pearson *et al.* (2003) evaluated factors that influenced growth and mortality of 6 pioneer tree species in forest gaps of different sizes in Panama. They found that herbivory varied from 2% to 10% overall, with *Croton bilbergianus* showing levels of 5–30%. Most species showed a trend of increasing leaf area loss with increasing gap size, but the fastest-growing species did not have the highest levels of herbivory. Variation in growth rate and mortality of these plant species could not be explained by foliage losses to herbivores but was strongly influenced by a tradeoff between maximum growth in the wet season and ability to survive seasonal drought, particularly in small gaps.

The rapid replacement of primary production lost to herbivores in many aquatic systems is well-known (Carpenter and Kitchell 1984, 1987, 1988, Carpenter *et al.* 1985, J. Wallace and O'Hop 1985). J. Wallace and O'Hop (1985) reported that new leaves of water lilies, *Nuphar luteum,* disappeared within 3 weeks as a result of grazing by the leaf beetle, *Pyrrhalta nymphaeae.* A high rate of leaf production was necessary to maintain macrophyte biomass. Trumble *et al.* (1993) reviewed literature demonstrating that compensatory growth (replacement of consumed tissues) following low to moderate levels of herbivory is a widespread response by terrestrial plants as well. Increased productivity of grazed grasses, compared to ungrazed grasses, has been demonstrated experimentally in a variety of grassland ecosystems (Belovsky and Slade 2000, Detling 1987, 1988, McNaughton 1979, 1986, 1993a, Seastedt 1985, S. Williamson *et al.* 1989), but growth enhancement may depend on the presence of herbivore feces (Baldwin 1990, Hik and Jefferies 1990) or other herbivore products (Baldwin 1990). M. Dyer *et al.* (1995) demonstrated that crop and midgut extracts present in grasshopper regurgitants during feeding stimulate coleoptile growth in grasses, but saliva may not stimulate growth of all plant species (Detling *et al.* 1980). Wickman (1980) and Alfaro and Shepherd (1991) reported that short-term growth losses by defoliated conifers were followed by several years, or even decades, of growth rates that exceeded predefoliation rates (Fig. 12.4). Romme *et al.* (1986) found that annual wood production in pine forests in western North America reached or exceeded preoutbreak levels within 10–15 years following mountain pine beetle, *Dendroctonus ponderosae,* outbreaks.

Detling (1987, 1988), M. Dyer *et al.* (1993, 1995), McNaughton (1979, 1986, 1993a), and Paige and Whitham (1987) have argued that herbivory may benefit some plants to the extent that species adapted to replace consumed tissues often disappear in the absence of grazing. NPP of some grasslands declines when grazing is precluded, as a result of smothering of shoots as standing dead material accumulates (Kinyamario and Imbamba 1992, Knapp and Seastedt 1986,

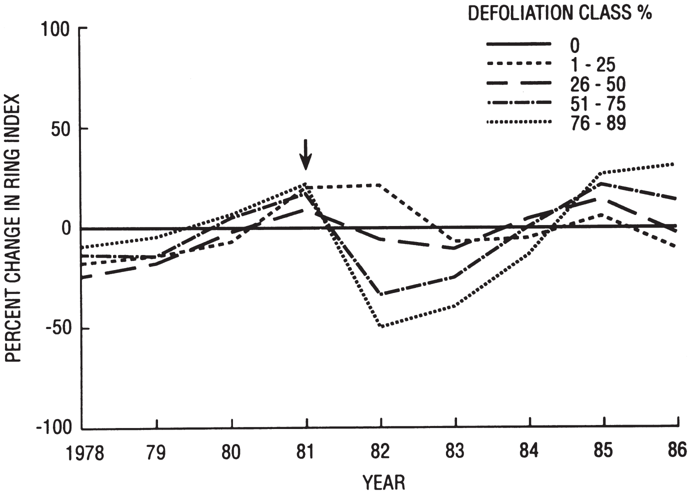


FIG. 12.4 Changes in ring width indices for Douglas-fir defoliated at different intensities by the Douglas-fir tussock moth, *Orgyia pseudotsugata,* in 1981 *(arrow)*. The horizontal line at 0% represents ring width index for nondefoliated trees. From Alfaro and Shepherd (1991) with permission from the Society of American Foresters. Please see extended permission list pg 572.

McNaughton 1979). D. Inouye (1982) reported that herbivory by several insect and mammalian herbivores had a variety of positive and negative effects on fitness of a thistle, *Jurinea mollis.*

These observations generated the *herbivore optimization hypothesis* (Fig. 12.5), or *overcompensation hypothesis,* that primary production is maximized at low to moderate levels of herbivory (Carpenter and Kitchell 1984, Mattson and Addy 1975, McNaughton 1979, Pedigo *et al.* 1986). This hypothesis is widely recognized among aquatic ecologists as the basis for inverted biomass pyramids (Carpenter and Kitchell 1984, 1987, 1988, Carpenter *et al.* 1985). Its application to terrestrial systems has been challenged (e.g., Belsky 1986, Painter and Belsky 1993, D. Patten 1993) but has been supported by experimental tests for both insect and vertebrate herbivores in grassland (Belovsky and Slade 2000, Detling 1987, M. Dyer *et al.* 1993, McNaughton 1979, 1993b, Seastedt 1985), salt marsh (Hik and Jefferies 1990), forest (Lovett and Tobiessen 1993, Schowalter *et al.* 1991), and even agricultural (Pedigo *et al.* 1986) ecosystems.

Compensatory growth likely depends on environmental conditions, availability and balances of limiting nutrients, timing of herbivory, and plant adaptation to herbivory (de Mazancourt *et al.* 1998, Loreau 1995, Trlica and Rittenhouse 1993, S. Williamson *et al.* 1989). C. Lovelock *et al.* (1999) demonstrated that CO_2 enrichment did not enhance compensation by a tropical legume, *Copaifera aromatica,* compared to compensation under ambient atmospheric CO_2, following artificial defoliation in Panama. Rastetter *et al.* (1997) used a multi-element model to demonstrate that plant response to CO_2 enrichment could be constrained by nitrogen limitation. De Mazancourt *et al.* (1998) and Loreau (1995) used a theoretical model to study conditions under which grazing optimization could occur. They found that grazing optimization required that moderate her-

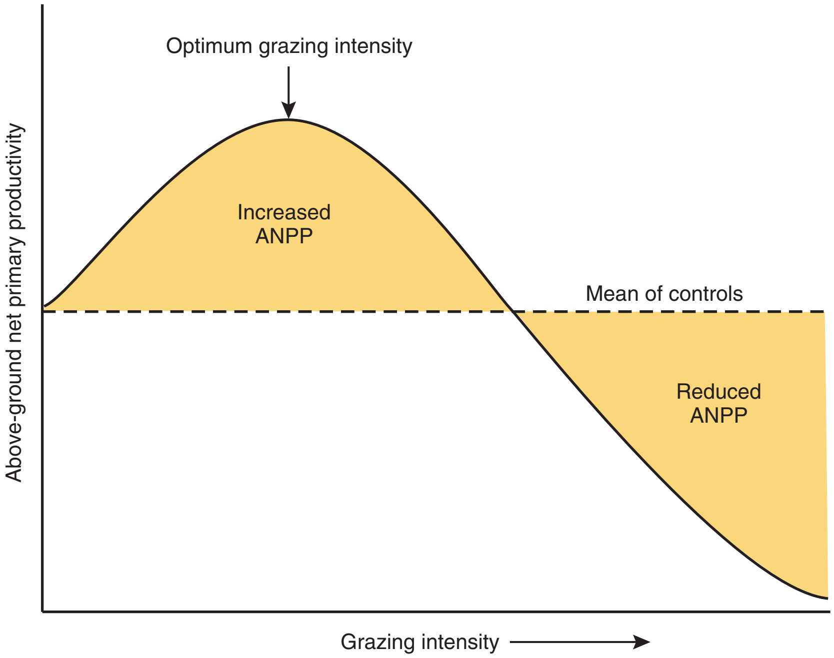


FIG. 12.5 Relationship between intensity of phytophagy and net primary production. Net primary production often peaks at low to moderate intensities of phytophagy, supporting the grazing optimization hypothesis. From S. Williamson *et al.* (1989) with permission from the Society for Range Management.

bivory decreased nutrient losses from the system. They concluded that grazing optimization is most likely to occur in ecosystems with large losses of limiting nutrients during decomposition or where herbivores import nutrients from outside the ecosystem.

Plants often are able to compensate for herbivory in the spring when conditions favor plant productivity but become less able to compensate later in the season (Akiyama *et al.* 1984, Hik and Jefferies 1990, Thompson and Gardner 1996). Grasshopper, *Aulocara elliotti,* did not significantly reduce standing crop of blue grama grass, *Bouteloua gracilis,* when feeding occurred early in the growing season but significantly reduced standing crop when feeding occurred later in southwestern New Mexico, United States (Thompson and Gardner 1996).

M. Dyer *et al.* (1991) reported that grazing-adapted and nongrazing-adapted clones of an African C_4 grass, *Panicum coloratum,* differed significantly in their responses to herbivory by grasshoppers. After 12 weeks of grazing, the grazing-adapted plants showed a 39% greater photosynthetic rate and 26% greater biomass, compared to the nongrazing-adapted plants. Lovett and Tobiessen (1993) found that experimental defoliation resulted in elevated photosynthetic rates of red oak, *Quercus rubra,* seedlings grown under conditions of low and high nitrogen availability but that high nitrogen seedlings were able to maintain high photosynthetic rates for a longer time (Fig. 12.6). Vanni and Layne (1997)

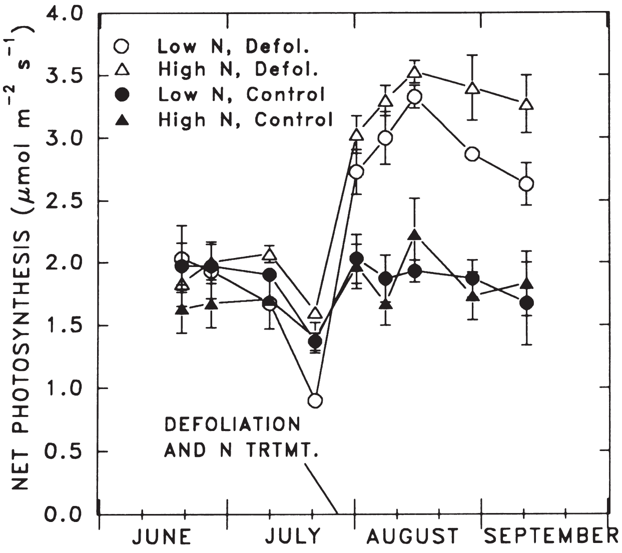


FIG. 12.6 Mean net photosynthetic rate in old leaves from *Quercus rubra* seedlings subjected to four combinations of nitrogen fertilization and defoliation intensity. Defoliation and fertilization treatments began July 26. From Lovett and Tobiessen (1993) with permission from Heron Publishing.

reported that consumer-mediated nutrient cycling strongly affected phytoplankton production and community dynamics in lakes.

Honkanen *et al.* (1994) artificially damaged needles or buds of Scots pine. Damage to buds increased shoot growth. Damage to needles stimulated or suppressed shoot growth, depending on the degree and timing of damage and the position of the shoot relative to damaged shoots. Growth was significantly reduced by loss of 100%, but not 50%, of needles and was significantly reduced on shoots located above damaged shoots, especially late in the season. Shoots located below damaged shoots showed increased growth. Honkanen *et al.* (1994) suggested that these different effects of injury indicated an important effect of physiological status of the damaged part (i.e., whether it was a sink [bud] or source [needle] for resources).

Morón-Ríos *et al.* (1997a) reported that below-ground herbivory by root-feeding scarab beetle larvae, *Phyllophaga* sp., prevented compensatory growth in response to above-ground grazing. Furthermore, salivary toxins or plant pathogens injected into plants by some sap-sucking species can cause necrosis of plant tissues (C. Jones 1984, Miles 1972, Raven 1983, Skarmoutsos and Millar 1982), honeydew accumulation on foliage can promote growth of pathogenic fungi and limit photosynthesis (Dik and van Pelt 1993), and some leaf miners induce premature abscission (Chabot and Hicks 1982, Faeth *et al.* 1981, Pritchard and James 1984a, b, Stiling *et al.* 1991), thereby exacerbating the direct effects of herbivory. However, foliage injury can induce resistance to subsequent herbivory or infection by plant pathogens (Hatcher *et al.* 1995, M. Hunter 1987, Karban and Baldwin 1997; see Chapters 3 and 8). Although primary productivity may be increased by low to moderate intensities of grazing, some plant tissues may be sacrificed by plant allocation of resources to replace lost foliage. Morrow and LaMarche (1978) and Fox and Morrow (1992) reported that incremental growth of *Eucalyptus* stems treated with insecticide was 2–3 times greater than that of unsprayed stems. Root growth and starch reserves are affected significantly by above-ground, as well as below-ground, herbivory. Morón-Ríos *et al.* (1997a) noted that root-feeders reduced root-to-shoot ratios by 40% and live-to-dead above-ground biomass ratio by 45% through tiller mortality, apparently reducing plant capacity to acquire sufficient nutrients for shoot production. Rodgers *et al.* (1995) observed that starch concentrations in roots were related inversely to the level of mechanical damage to shoots of a tropical tree, *Cedrela odorata* (Fig. 12.7). Gehring and Whitham (1991, 1995) reported that folivory on pinyon pine adversely affected mycorrhizal fungi, perhaps through reduced carbohydrate supply to roots. However, Holland *et al.* (1996) reported that grasshopper

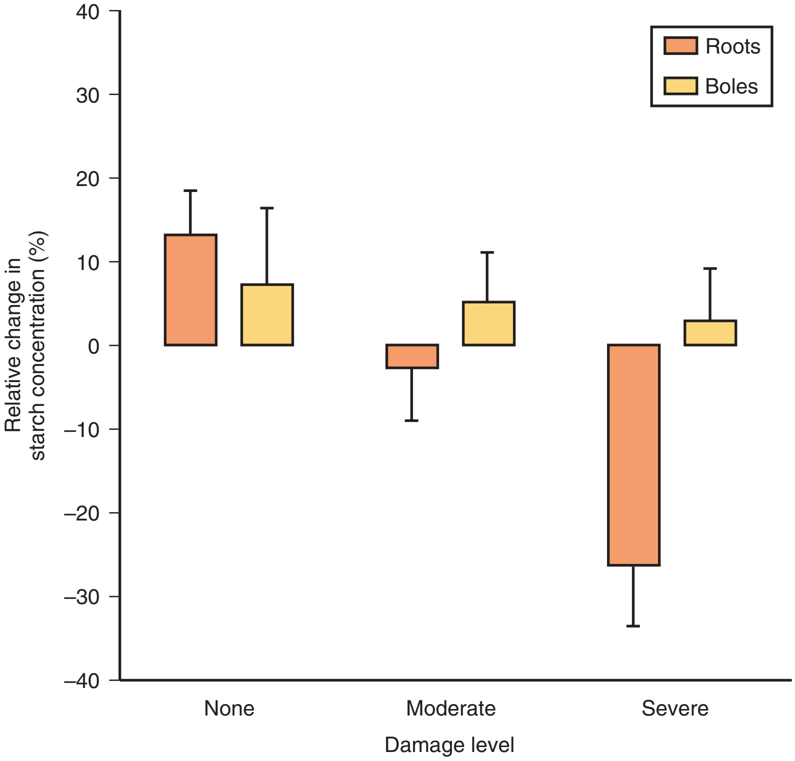


FIG. 12.7 Effect of intensity of artificial herbivory (to simulate terminal shoot damage by a lepidopteran, *Hypsipyla grandella)* on mean relative change (+ standard error) in starch concentrations (percent of initial level) in roots and lower boles of a neotropical hardwood, *Cedrela odorata,* in Costa Rica. In the moderate treatment, 0.2–0.3 cm of terminal shoot was excised; in the severe treatment, 0.5–0.6 cm of terminal was excised. Data represent 5 sampling dates over a 12-day period beginning 18 days after treatment. From Rodgers *et al.* (1995) with permission from the Association of Tropical Biologists.

grazing on maize increased carbon allocation to roots. Soil microbial biomass peaked at intermediate levels of herbivory in no-tillage agricultural systems (Holland 1995), perhaps because moderate intensities of herbivory increased root exudates that fuel microbial production (Holland *et al.* 1996). McNaughton (1979, 1993a) and van der Maarel and Titlyanova (1989) concluded that sufficient shoot biomass to maintain root function is critical to plant ability to compensate for losses to herbivores.

Levels of herbivory that exceed plant ability to compensate lead to growth reduction, stress, and mortality. Seedlings are particularly vulnerable to herbivores because of their limited resource storage capacity and may be unable to replace tissues lost to herbivores (P. Hulme 1994, Wisdom *et al.* 1989). D. Clark and Clark (1985) reported that survival of tropical tree seedlings was highly correlated with the percentage of original leaf area present 1 month after germination and with the number of leaves present at 7 months of age. Continued grazing during periods of reduced plant productivity generally exacerbates stress. Resource-limited plants are more likely to succumb to herbivores than are plants with optimal resources (Belovsky and Slade 2000, Lovett and Tobiessen 1993). Plant species most stressed by adverse conditions suffer severe mortality to herbivores (e.g., Crawley 1983, Painter and Belsky 1993, Schowalter and Lowman 1999). Wright *et al.* (1986) found that Douglas-fir beetle, *Dendroctonus pseudotsugae,* and fir engraver beetle, *Scolytus ventralis,* preferentially colonized Douglas-fir trees that had lost >90% of foliage to Douglas-fir tussock moth although larval survival was greater in nondefoliated than in defoliated trees. However, Kolb *et al.* (1999) demonstrated that intense defoliation could reduce moisture stress during dry periods (see earlier in this chapter).

Herbivory by exotic species may cause more severe or more frequent reduction in productivity and survival, in part because plant defenses may be less effective against newly associated herbivores. The most serious effects of herbivory, however, result from artificially high intensities of grazing by livestock or game animals (Oesterheld *et al.* 1992, D. Patten 1993). Whereas grazing by native herbivores usually is seasonal and grasses have sufficient time to replace lost tissues before grazing resumes, grazing by livestock is continuous, allowing insufficient time for recovery (McNaughton 1993a, Oesterheld and McNaughton 1988, 1991, Oesterheld *et al.* 1992).

Herbivory also can alter plant architecture, potentially influencing future growth and susceptibility to herbivores. Gall-formers deform expanding foliage and shoots. Repeated piercing during feeding-site selection by sap-sucking species also can cause deformation of foliage and shoots (Miles 1972, Raven 1983). Shoot-borers and bud-feeders kill developing shoots and induce growth of lateral shoots (D. Clark and Clark 1985, Nielsen 1978, Reichle *et al.* 1973, Zlotin and Khodashova 1980). Severe or repeated herbivory of this type often slows or truncates vertical growth and promotes bushiness. Gange and Brown (1989) reported that herbivory increased variation in plant size. Morón-Ríos *et al.* (1997a) found that both above-ground and below-ground herbivory alter shoot-to-root ratios. Suppression of height or root growth restricts plant ability to acquire resources and often leads to plant death. However, pruning also can stimulate growth and seed production (e.g., D. Inouye 1982) or improve water and nutrient balance (e.g., W. Webb 1978).

B. Community Dynamics

Differential herbivory among plants and plant species in an ecosystem affects both the distribution of individuals of a particular plant species and the opportunities for growth of plant species resistant to or tolerant of herbivory. The intensity of herbivory determines its effects on plant communities. Low to moderate intensities that prevail most of the time generally ensure a slow turnover of plant parts or individual plants. High intensities during outbreaks or as a result of management can dramatically reduce the abundance of preferred species and rapidly alter vegetation structure and composition. However, D. Inouye (1982) and Paige and Whitham (1987) demonstrated that herbivory can increase seed production.

Overgrazing by domestic livestock has initiated desertification of arid grasslands (by reducing vegetation cover, causing soil desiccation) in many parts of the globe (e.g., Schlesinger *et al.* 1990). Herbivory by exotic insect species (but rarely native species) is capable of eliminating plant species that are unable to compensate (McClure 1991). Patterns of herbivory often explain observed geographic or habitat distributions of plant species (Crawley 1983, 1989, Huntly 1991, Louda *et al.* 1990a, Schowalter and Lowman 1999). Herbivory has a variety of positive and negative effects on plant growth and fitness, even for a particular plant species (D. Inouye 1982; see earlier in this chapter). Herbivory can prevent successful establishment or continued growth, especially during the vulnerable seedling stage (D. Clark and Clark 1985, P. Hulme 1994, Wisdom *et al.* 1989). Louda *et al.* (1990a) reported that patterns of herbivory on two species of goldenbushes, *Happlopappus* spp., explained the significant difference between expected and observed distributions of these species across an environmental gradient from maritime to interior ecosystems in southern California (Fig. 12.8). Louda and Rodman (1996) found that chronic herbivory by insects was concentrated on bittercress, *Cardamine cordifolia,* growing in sunny habitats and largely explained the observed restriction of this plant species to shaded habitats. Schowalter *et al.* (1981a) suggested that differential mortality among pine species (as a result of southern pine beetle, *Dendroctonus frontalis*) in the southern United States largely explained the historic patterns of species distributions over topographic gradients.

Herbivory on dominant plant species can promote persistence of associated plant species. Sousa *et al.* (2003) found that predation by a scolytid beetle, *Coccotrypes rhizophorae,* on seedlings of the mangrove, *Rhizophora mangle,* prevented establishment of *R. mangle* in lightning-generated gaps and permitted a shade-intolerant species, *Laguncularia racemosa,* to co-dominate the mangrove community on the Caribbean coast of Panama. McEvoy *et al.* (1991) documented changes in plant community structure resulting from herbivore-induced mortality to the exotic ragwort, *Senecio jacobeae,* in western Oregon. Ragwort standing crop declined from $>700\,\mathrm{g\,m^{-2}}$ (representing 90% of total standing crop of

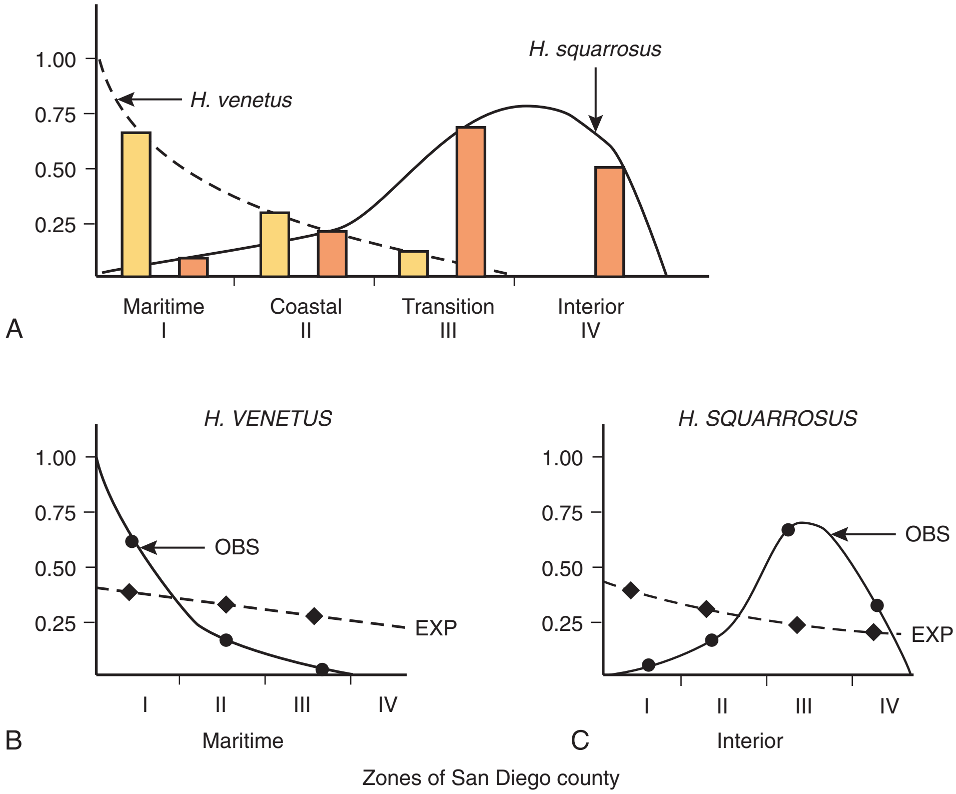


FIG. 12.8 Herbivore effects on plant species distribution. **A:** Gradients in observed frequencies of two goldenbushes, *Happlopappus venetus (yellow)* and *H. squarrosus (orange)*, from maritime to interior montane sites in San Diego County, California. **B and C:** Observed frequency accounting for herbivore effects *(solid lines)* compared to potential distribution in the absence of herbivory *(dashed line)* based on several measures of performance of control plants when insects were excluded. From Louda *et al.* (1990a). Please see extended permission list pg 572.

vegetation) to 0.25 g m^{-2} over a 2-year period following release of the ragwort flea beetle, *Longitarsus jacobaeae.* Grasses responded rapidly to declining ragwort abundance, followed by forbs, resulting in relatively constant vegetation standing crop over the 8 years of measurement.

Herbivory often facilitates successional transitions (see Chapter 10). Selective herbivory among plant species suppresses those on which herbivory is focused and provides space and other resources to others, resulting in altered plant community composition (e.g., Davidson 1993, McEvoy *et al.* 1991, Schowalter 1981, Schowalter *et al.* 1986). V.K. Brown and Gange (1989), V.K. Brown *et al.* (1988), and Gibson *et al.* (1990) reported that chemically reduced above-ground herbivory resulted in lower plant species richness after 2 years, whereas V.K. Brown and Gange (1989) found that reduced below-ground herbivory resulted in higher plant species richness, largely reflecting differential intensities of herbivory among various grass and forb species. V. Anderson and Briske (1995) simulated herbivory by livestock in a transplant garden containing mid-seral and late-seral grass species to test alternative hypotheses that (1) mid-seral species have greater tolerance to herbivory or (2) herbivory is focused on late-seral species to explain species replacement in intensively grazed grasslands in the southern United States. They found that late-seral species had greater competitive ability and equivalent or higher tolerance to herbivory, indicating that selective herbivory on the late-successional species is the primary mechanism for reversal of succession (i.e., return to dominance by mid-seral species under intense grazing pressure). Conversely, Bach (1990), Coley (1980, 1982, 1983), Coley and Aide (1991), and Lowman and Box (1983) reported that intensities of herbivory by insects were higher in earlier successional stages than in later successional stages. Schowalter *et al.* (1981a) suggested that southern pine beetle is instrumental in advancing succession in the absence of fire by selectively killing early successional pines, thereby favoring their replacement by later successional hardwoods (see Fig. 10.5).

Davidson (1993) compiled data indicating that herbivores may retard or reverse succession during early seres but advance succession during later seres. She suggested that herbivory is concentrated on the relatively less defended, but grazing tolerant, mid-successional grasses, forbs, and pioneer trees (see Bach 1990). Increased herbivory at early stages of community development tends to retard succession, whereas increased herbivory at later stages advances succession. Environmental conditions may affect this trend. For example, succession from pioneer pine forest to late successional fir forest in western North America can be retarded or advanced, depending primarily on moisture availability and condition of the dominant vegetation. Under conditions of adequate moisture (riparian corridors and high elevations), mountain pine beetle advances succession by facilitating the replacement of host pines by the more shade-tolerant, fire-intolerant, understory firs. However, limited moisture and short fire return intervals at lower elevations favor pine dominance. In the absence of fire during drought periods, herbivory by several defoliators and bark beetles is concentrated on the understory firs, truncating (or reversing) succession. Fire fueled by fir mortality also leads to eventual regeneration of pine forest. Similarly, each plant species that became dominant during succession following Hurricane Hugo in Puerto Rico induced elevated herbivory that facilitated its demise and replacement (Torres 1992). The direction of succession then depends on which plant species are present and their responses to environmental conditions.

Changes in plant condition, community composition, and structure affect habitat and food for other animals and microorganisms. Changes in nutritional quality or abundance of particular foliage, fruit, or seed resources affect abundances of animals that use those resources. Animals that require or prefer nesting cavities in dead trees may be promoted by tree mortality resulting from herbivore outbreaks.

Grazing on above-ground plant parts can affect litter and rhizosphere processes in a variety of ways (Bardgett *et al.* 1998). Reduced foliar quality resulting from induced defenses or replacement of palatable by less palatable plant species can reduce the quality of detrital material (Fig. 12.9). Seastedt *et al.* (1988)

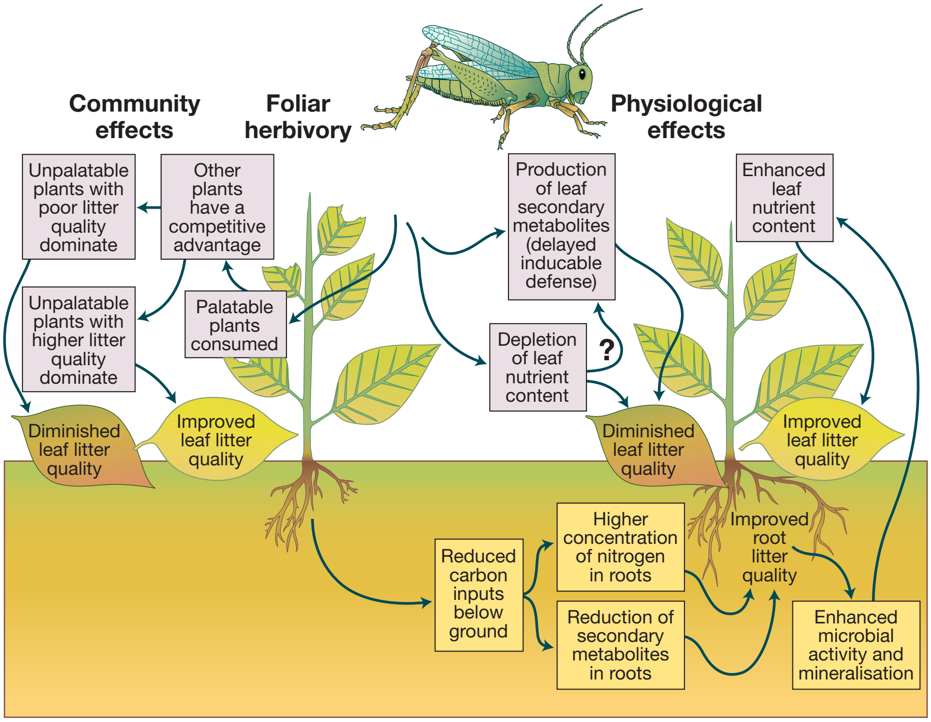


FIG. 12.9 Effects of herbivory on host nutrient allocation and trophic interactions. From Bardgett *et al.* (1998) with permission from Elsevier Science.

reported that simulation of herbivore effects on throughfall (precipitation enriched with nutrients while passing over foliage) affected litter arthropod communities. Schowalter and Sabin (1991) found that three taxa of litter arthropods were significantly more abundant under experimentally defoliated (≤20% foliage eaten) Douglas-fir saplings, compared to nondefoliated saplings. Reynolds *et al.* (2003) experimentally evaluated effects of herbivore-derived litter components on litter invertebrates. They found that addition of herbivore feces increased abundances of Collembola and fungal- and bacterial-feeding nematodes; addition of throughfall increased abundances of fungal- and bacterial-feeding nematodes; litterfall exclusion reduced abundances of oribatid and prostigmatid mites. Altered carbon storage in roots (Filip *et al.* 1995, Holland *et al.* 1996) affects resources available for below-ground food webs (Fig. 12.10). Bardgett *et al.* (1997, 1998) reported that microbial biomass, nematode abundance, and soil respiration rates were consistently reduced by removal of sheep grazing (Fig. 12.11). Gehring and Whitham (1991, 1995) documented significantly reduced mycorrhizal activity on roots of piñon pines subject to defoliation by insects compared to nondefoliated pines.

Insect herbivores or their products constitute highly nutritious resources for insectivores and other organisms. Caterpillars concentrate essential nutrients several orders of magnitude over concentrations in foliage tissues (e.g., Schowalter and Crossley 1983). Abundances of insectivorous birds and mammals often increase in patches experiencing insect herbivore outbreaks (Barbosa and

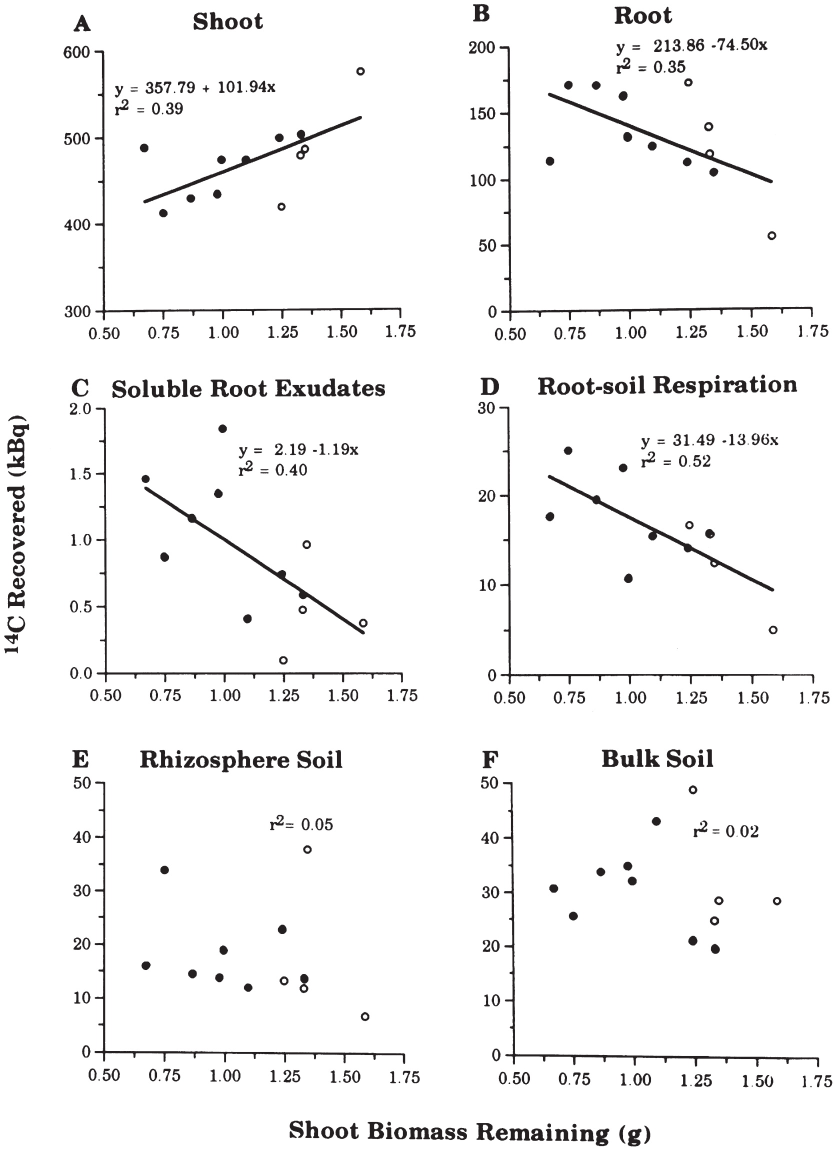
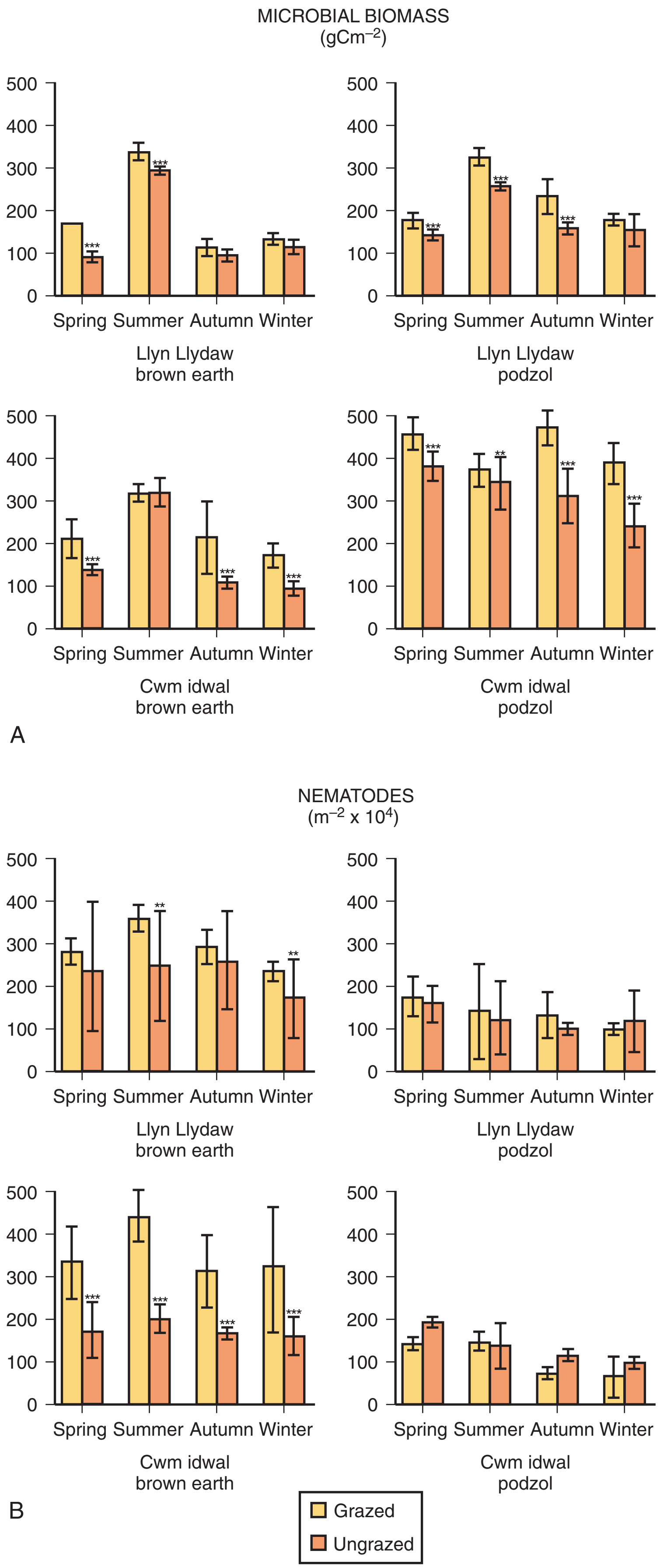


FIG. 12.10 Carbon allocation as a function of intensity of herbivory (measured as shoot biomass remaining) in **A:** shoots, **B:** roots, **C:** soluble root exudates, **D:** respiration from roots and soil, **E:** rhizosphere soil, and **F:** bulk soil. Data were normalized for differences in $^{14}CO_2$ uptake; 1 kBq = 1000 disintegrations sec^{-1}. Shoot biomass was inversely related to leaf area removed by herbivores. Regression lines are shown where significant at $P < 0.05$. Open circles represent ungrazed plants, and solid circles represent grazed plants. From Holland *et al.* (1996) with permission from Springer-Verlag. Please see extended permission list pg 572.


MICROBIAL BIOMASS
(gCm−2)
500
400
300
200
100
0
Spring Summer Autumn Winter
***
**
Llyn Llydaw
brown earth
Llyn Llydaw
podzol
Cwm idwal
brown earth
Cwm idwal
podzol
A
NEMATODES
(m−2 x 104)
B
Grazed
Ungrazed

Wagner 1989). Arthropod tissues also represent concentrations of nutrients for decomposers (Schowalter and Crossley 1983, Seastedt and Tate 1981).

A variety of organisms use honeydew accumulation from aphids, scales, and other Homoptera. Ants, honey bees, *Apis mellifera*, hummingbirds, and other animals forage on the carbohydrate-rich honeydew (N. Edwards 1982). Stadler and Müller (1996) and Stadler *et al.* (1998) reported that the presence of honeydew significantly increased the growth of a variety of epiphytic bacteria, yeasts, and filamentous fungi on the surface of conifer needles, potentially affecting photosynthetic efficiency of underlying foliage.

C. Water and Nutrient Fluxes

Relatively few studies have addressed effects of insect herbivores on biogeochemical cycling processes, despite herbivore effects on plant chemistry and the importance of vegetation and litter structure, and turnover of material between these pools, to biogeochemical cycling. Crossley and Howden (1961) pioneered the study of nutrient fluxes from vegetation through arthropod communities and demonstrated that insect herbivores concentrate and accelerate cycling of some nutrients. Subsequent research has demonstrated that insect herbivores affect biogeochemical cycling in a number of ways, including altered vegetation composition and structure, direct transfer of material from plants to litter, and effects on litter quality and litter communities.

Altered vegetation composition changes patterns of acquisition and turnover of various nutrients by the vegetation. For example, insects (such as bark beetles) that affect the relative composition of Douglas-fir and western redcedar, *Thuja plicata,* in the northwestern United States affect calcium dynamics and soil pH (i.e., calcium accumulation and higher pH under western redcedar compared to Douglas-fir; e.g., Kiilsgaard *et al.* 1987). Similarly, Ritchie *et al.* (1998) reported that herbivory generally reduced the abundance of plant species with N-rich tissues, leading to replacement by plant species with lower N concentrations, in an oak savanna in the north central United States.

Reduced metabolic demands by pruned or defoliated plants can reduce water and nutrient uptake (W. Webb 1978) and potentially contribute to plant survival during drought periods (Kolb *et al.* 1999). W. Webb and Karchesy (1977) reported that defoliation by the Douglas-fir tussock moth reduced host starch content proportional to defoliation intensity. Reallocation of carbon by plants, as a result of herbivory, alters carbon cycling and energy flux.

Herbivory affects biogeochemical cycling directly by changing the timing, amount, and form of nutrients transferred from plants to litter or soil. In the absence of herbivory, litter accumulation may be highly seasonal (i.e.,

FIG. 12.11 Seasonal variation in microbial biomass and nematode abundance in grazed and ungrazed plots of two grassland types in Ireland. Vertical lines represent standard errors; *, $P < 0.05$, **, $P < 0.01$; ***, $P < 0.001$. From Bardgett *et al.* (1997) with permission from Elsevier Science.

concentrated at the onset of cold or dry conditions) and have low nutrient concentrations (especially of nitrogen or other nutrients that are resorbed from senescing foliage; Marschner 1995). Herbivory increases the amount and nutrient content of litter inputs during the growing season by transferring nutrients in fragmented plant material, insect tissues, and insect feces. Increased nutrient content and defenses induced by herbivory affect the quality of such litter for decomposers (e.g., S. Chapman *et al.* 2003, Coley and Barone 1996, Fonte and Schowalter 2004, M. Hunter *et al.* 2003). Insect tissues and feces have higher concentrations of nutrients that control litter decomposition than does senescent leaf litter (M. Hunter *et al.* 2003, Schowalter and Crossley 1983). Hollinger (1986) reported that during an outbreak of the California oak moth, *Phryganidia californica,* fluxes of nitrogen and phosphorus from trees to the ground more than doubled, and feces and insect remains accounted for 60–70% of the total nitrogen and phosphorus fluxes. J.R. Grace (1986) found similar increase in nitrogen flux from 31 kg N ha^{-1} in nondefoliated forest to 52 kg N ha^{-1} in forest defoliated by gypsy moth, *Lymantria dispar,* in Pennsylvania, United States.

Folivory also increases the flux of nutrients in the form of throughfall (precipitation enriched with nutrients as it percolates through the canopy). Throughfall nutrient fluxes from canopy to litter are controlled strongly by foliage area, exposed surfaces resulting from herbivory, and amount of precipitation (Lovett *et al.* 1996). M. Hunter *et al.* (2003), Kimmins (1972), Schowalter *et al.* (1991), Seastedt *et al.* (1983), and Stachurski and Zimka (1984) have shown that herbivory greatly increases leaching of nutrients from chewed foliage (Fig. 12.12). However, in ecosystems with high annual precipitation, herbivore-induced nutrient turnover may be masked by nutrient inputs via precipitation (Schowalter *et al.* 1991).

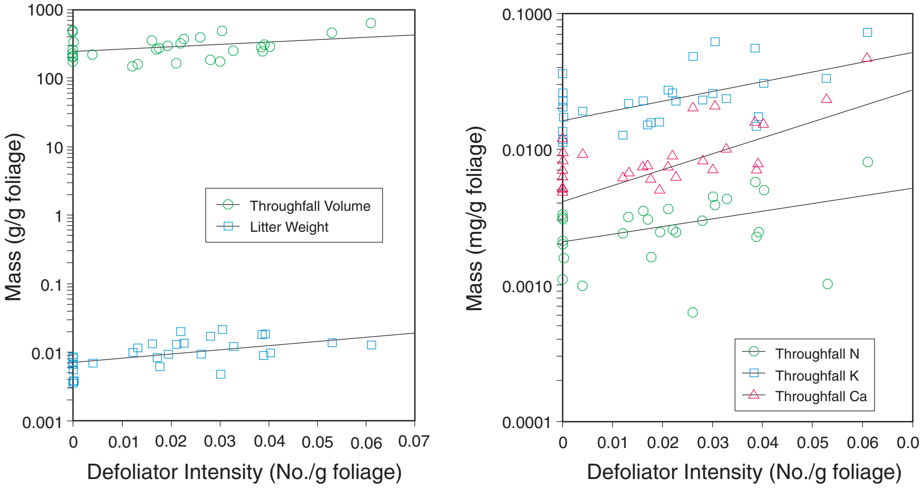


FIG. 12.12 Folivore effects on throughfall, litterfall, and fluxes of N, K, and Ca from young Douglas fir during the feeding period, April–June, in western Oregon. From Schowalter *et al.* (1991) with permission from Elsevier Science.

The contribution of honeydew to nutrient cycling has been a subject of considerable interest. Stadler and Müller (1996) and Stadler *et al.* (1998) documented significant amounts of dissolved organic carbon in aphid honeydew. Most of the honeydew in their studies was immobilized quickly by phylloplane microorganisms before reaching the ground. Owen (1978) and Owen and Wiegert (1976) suggested that the trisaccharide, melezitose, in aphid honeydew provides a rich, labile carbohydrate resource for free-living, nitrogen-fixing soil bacteria. Petelle (1980) subsequently demonstrated that fructose, also abundant in aphid honeydew, increased nitrogen fixation nine-fold more than did melezitose. However, Grier and Vogt (1990) found that chemical removal of aphids increased available soil nitrogen, nitrogen mineralization rates, NPP, and nitrogen uptake by red alder (*Alnus rubra*). These data, together with those of Lovett and Ruesink (1995), indicate that nutrients mobilized by folivores and sap-suckers may be immobilized rapidly by soil microorganisms.

Several studies have experimentally addressed the effect of herbivore-derived inputs on decomposition, soil nutrient fluxes, and nutrient uptake by plants. Throughfall, senescent foliage, fresh foliage fragments lost via herbivory (greenfall), and herbivore feces differ in the amount and form of nitrogen and carbon compounds, as well as in the degree of microbial preconditioning. Fonte and Schowalter (2004) demonstrated that fresh foliage of four tropical tree species in Puerto Rico had higher nitrogen concentration and decomposed significantly more rapidly than did senescent foliage from the same tree species. Zlotin and Khodashova (1980) reported that herbivore feces decomposed more rapidly than did raw plant material. M. Hunter *et al.* (2003) found that deposition of folivore feces explained 62% of the variation in soil nitrate availability.

Lovett and Ruesink (1995) reported that gypsy moth feces contained much labile carbon and nitrogen but that microbial growth, stimulated by labile carbon (Fig. 12.13), was sufficient to immobilize all the available nitrogen (Fig. 12.14). In a subsequent experiment, Christenson *et al.* (2002) added ^{15}N-labeled leaf litter or gypsy moth feces to experimental plots, in which a red oak seedling had been planted, to evaluate pathways of nitrogen flux (Fig. 12.15). They found that gypsy moth feces significantly increased the concentration of ^{15}N in total and mineralizable nitrogen pools in surface and subsurface soils, with 40% of the recovered ^{15}N incorporated in soil. The red oak seedlings in plots with feces addition had significantly higher ^{15}N concentrations in green leaves, stems, and roots. By comparison, 80% of the ^{15}N in plots with added leaf litter remained in undecomposed leaves. Differences in amounts of ^{15}N recovered between the two treatments might reflect unmeasured gas fluxes or leaching of dissolved organic nitrogen. In contrast, Frost and Hunter (2004) and Fonte and Schowalter (2005) found that frass deposition in the southern Appalachians and in Puerto Rico, respectively, increased leaching of nitrate from forest soils. The difference in nitrogen mobilization between these two studies and those of Lovett and Ruesink (1995) and Christenson *et al.* (2002) may reflect particular herbivore-microbe-soil interactions (see Chapter 15).

Belovsky and Slade (2000) reported that grasshoppers, *Melanoplus sanguinipes,* accelerated nitrogen cycling by increasing the abundance and decom-

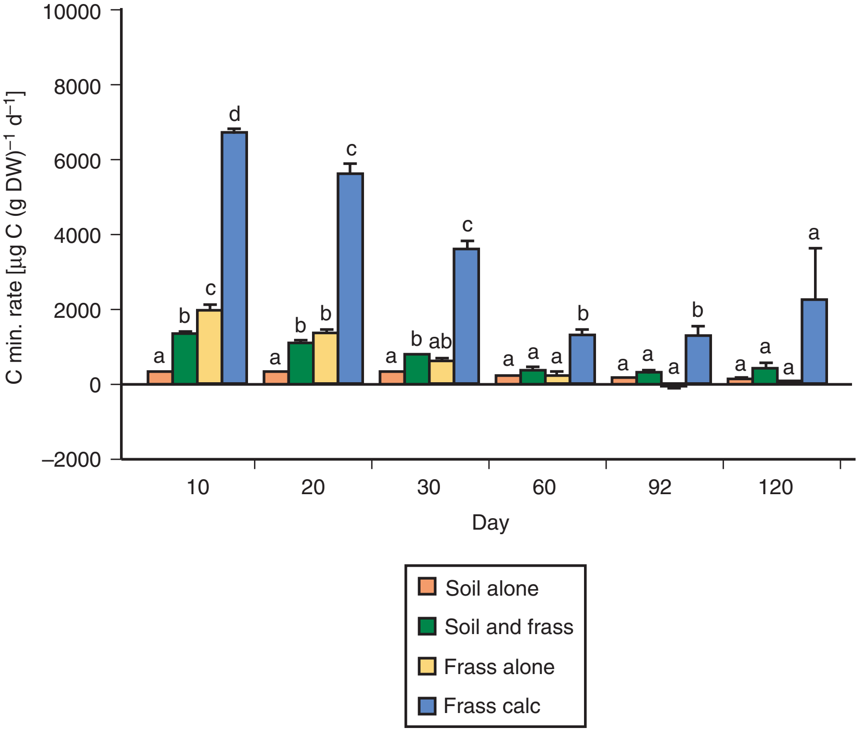


FIG. 12.13 Mean carbon mineralization rate (CO_2 evolution) in soil alone, soil + gypsy moth frass, and frass alone. Frass calc. was calculated by subtracting mean net C mineralization in soil alone from that in the soil + frass and expressing the rate per gram dry weight of frass. Vertical lines are standard errors. Within a sample date, bars under the same letter are not significantly different at $P < 0.05$. From Lovett and Ruesink (1995) with permission from Springer-Verlag. Please see extended permission list pg 572.

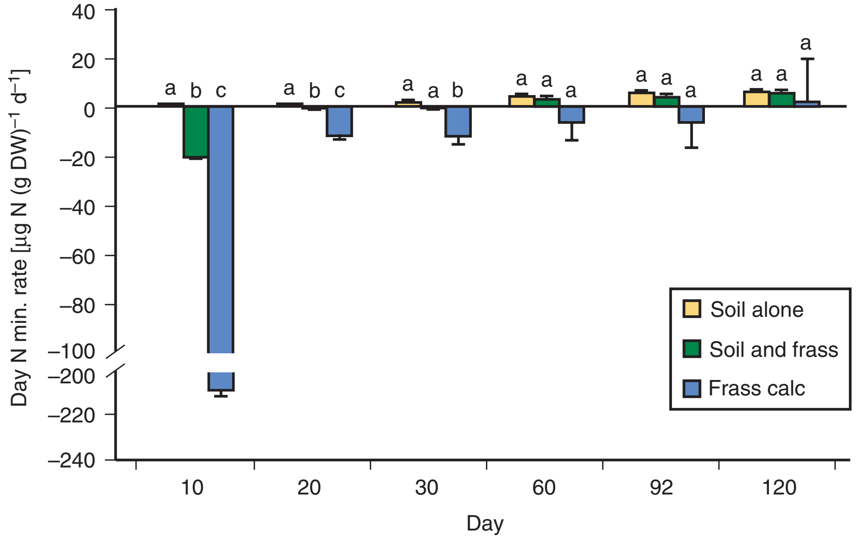


FIG. 12.14 Mean potential net nitrogen mineralization rate (extractable NH^{+}_{4} + NO^{-}_{3}) in soil alone, soil + gypsy moth frass, net and frass in soil + frass (see Fig. 12.13 for calculation of frass contribution). From Lovett and Ruesink (1995) with permission from Springer-Verlag. Please see extended permission list pg 572.

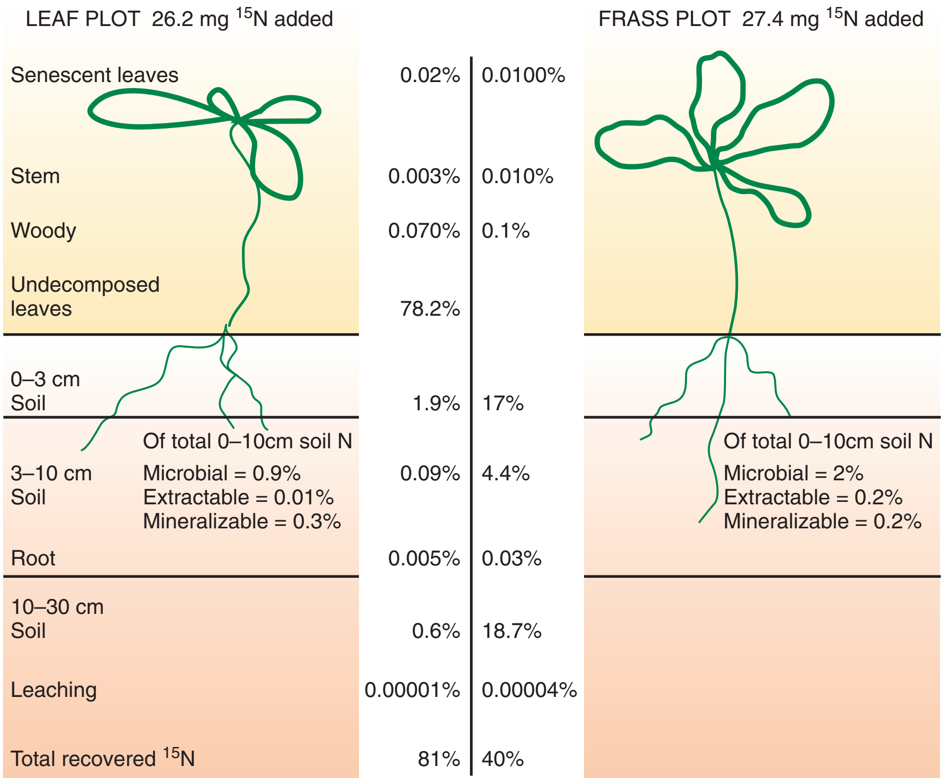


FIG. 12.15 Percent recovery of ^{15}N from various fractions, relative to the total amount added to plots as insect feces in June or as leaves at the time of leaf senescence in November. From Christenson *et al.* (2002) with permission from Elsevier. Please see extended permission list pg 572.

position rate of grass litter. Increased grasshopper density increased plant productivity up to 18%, especially by plants that are better competitors when nitrogen is more available, but high grasshopper densities depressed primary productivity.

S. Chapman *et al.* (2003) used a unique long-term herbivore exclusion experiment in Arizona, United States, to evaluate the effects of folivores and sap-suckers on foliage chemistry and decomposition. The shoot moth, *Dioryctria albovittella,* feeds on shoots and cones of mature pinyon pines, *Pinus edulis,* whereas the scale insect, *Matsucoccus acalyptus,* feeds only on needles of juvenile trees. Exclusion of both herbivores from experimental trees permitted comparison of susceptible, infested and uninfested trees, and resistant trees. Foliage litter chemistry was similar for resistant and susceptible uninfested trees, but both had significantly lower nitrogen concentration than did foliage litter of susceptible infested trees for both insect species, demonstrating that the insects were responsible for the increased nitrogen in litter. Furthermore, phosphorus concentration was significantly higher (by 50%) in litter from trees infested with scale insects, compared to resistant and susceptible uninfested trees. The scale insect, but not the moth, significantly increased the rate of litterfall from infested trees, relative to resistant and susceptible uninfested trees. Litter from resistant and susceptible infested trees was placed under each treatment type (Fig. 12.16). As expected, litter from susceptible, infested trees for both insects decomposed significantly more rapidly than did litter from resistant trees. For the scale treatments, both resistant and susceptible litter decomposed more rapidly under

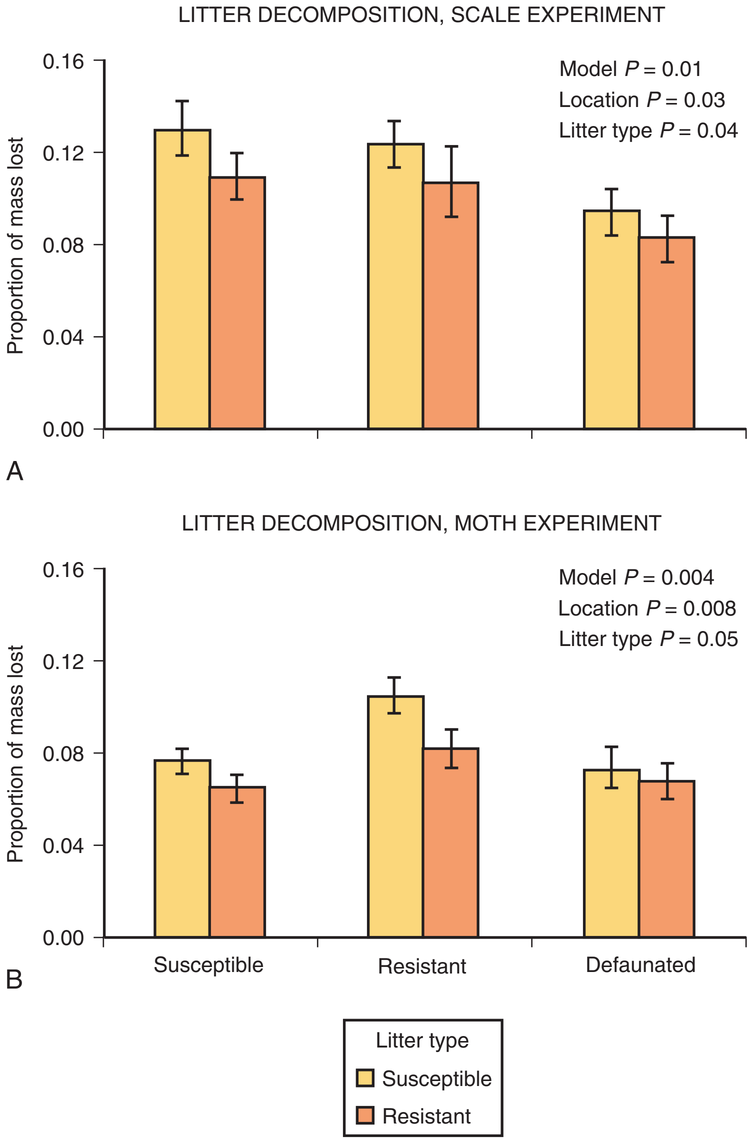


FIG. 12.16 Increased decomposition resulting from herbivore-induced changes in litter quality. Litter from susceptible or resistant pinyon pines was placed under susceptible, resistant, or experimentally defaunated trees. N = 20 for all treatments; vertical lines are standard errors. P values are given for main effects by 2-way ANOVA (analysis of variance). The two litter types did not differ within any location, but they did differ across all three locations. From S. Chapman *et al.* (2003) with permission from the Ecological Society of America. Please see extended permission list pg 572.

resistant and susceptible infested trees, compared to susceptible uninfested trees, perhaps because of higher throughfall, soil moisture, and soil temperature that were indirect effects of herbivory by scales. Litter from infested trees decomposed more rapidly under infested trees than did resistant litter under resistant trees. For moth treatments, both litter types decomposed more rapidly under resistant trees than under susceptible infested or uninfested trees; for unknown reasons litter from infested trees did not decompose more rapidly under infested trees than did resistant litter under resistant trees. However, because litter from moth-infested trees was higher quality and decomposed more rapidly across all treatments compared to resistant litter, higher rates of decomposition might be observed over longer time periods.

The shift in biomass dominance from folivores to sap-suckers following disturbance in temperate and tropical forests (Schowalter 1995, Schowalter and Ganio 1999, Schowalter *et al.* 1981c) indicates an accompanying shift in the predominant flux of nutrients. Dominance by folivores in undisturbed forests should transfer nutrients primarily as throughfall (enhanced by leaching from chewed foliage) and fragmented plant parts, whereas dominance by sap-suckers in early successional communities should transfer nutrients predominantly as a labile carbohydrate solution that stimulates microbial growth and immobilization of accompanying nutrients.

Herbivory has the capacity to alter nutrient cycling processes at the landscape or watershed level. Although most studies have addressed herbivore effects during outbreaks, nonoutbreak levels of herbivory can significantly affect fluxes (M. Hunter *et al.* 2003). MacDonald *et al.* (1992) attributed elevated nitrate concentrations in soil solution in hardwood forests in Michigan, United States, to defoliation by the forest tent caterpillar, *Malacosoma disstria.* Swank *et al.* (1981) reported that defoliation of hardwood forests by the fall cankerworm, *Alsophila pometaria,* in the southern Appalachian Mountains in North Carolina, United States, increased nitrate export via soil leaching and streamflow. Eshleman *et al.* (1998) and J. Webb *et al.* (1995) documented increased nitrate export in streams draining hardwood forests defoliated by the gypsy moth in the mid-Appalachian Mountains in Pennsylvania, Virginia, and West Virginia. However, Bormann and Likens (1979) reported no increase in nitrate export resulting from saddled prominent caterpillar, *Heterocampa guttivitta,* in the northern Appalachian Mountains in New Hampshire. Differences in results between these studies might reflect elevated nitrogen inputs throughout the northern Appalachians during the 1979s or different retention mechanisms among northern and southern study sites. Although most of the nitrogen consumed by folivores is retained by the ecosystem, even small increases in stream export of nitrate can alter water quality and leaching of nutrient cations such as Ca or toxic cations such as Al (Lovett *et al.* 2002).

D. Effects on Climate and Disturbance Regime

Herbivore-induced changes in vegetation structure likely affect soil temperature, relative humidity, erosion, soil moisture, and soil fertility (see Chapter 11). Changes in litter accumulation can affect ecosystem vulnerability or sensitivity to some disturbances, especially fire. However, relatively few studies have demonstrated herbivore effects on these variables. Herbivory increases vegetation porosity (Fig. 12.17) and penetration of light, precipitation, and wind to the understory and soil surface. Canopy opening greatly affects abiotic conditions in the understory (Chazdon and Fetcher 1984, Denslow 1995, Fernandez and Fetcher 1991). Increased soil warming as a result of penetration of sunlight may be offset to some extent by increased penetration of precipitation to the ground. Schowalter *et al.* (1991) reported that 20% loss of foliage mass doubled the amount of water reaching the soil surface. S. Chapman *et al.* (2003) also reported that herbivory by scale insects increased soil temperature and moisture. Reduced plant surface area reduces interception of precipitation and evapotranspiration (G. Parker 1983). Increased accumulation of litter resulting from herbivory in forest ecosystems may contribute to soil water retention.

Canopy opening over large areas by herbivores could affect regional climate. Although most studies of effects of canopy opening on climate have focused on anthropogenic canopy removal (see Chapter 11), herbivory may have similar effects (e.g., increased soil surface temperature, reduced evapotranspiration, and consequent regional warming and drying; J. Foley *et al.* 2003, Salati 1987).

FIG. 12.17 Increased canopy porosity resulting from herbivory. Holes chewed by folivorous insects in the large leaves of *Cecropia* increase the penetration of light, water, and airflow to lower strata.

Herbivory can increase or decrease the likelihood or severity of future disturbances. Herbivory in grasslands reduces the amount of standing dead material (Knapp and Seastedt 1986), potentially reducing the severity of fire but increasing soil exposure to desiccation and exacerbating effects of drought. However, reduced foliage surface area may reduce water demand and mitigate the effects of drought (Kolb *et al.* 1999). Herbivory in forests increases fuel accumulation in the form of fine and coarse litter material, thereby increasing the likelihood and severity of fire, especially in arid forests where litter decomposes slowly and lightning strikes are frequent (McCullough *et al.* 1998, Schowalter 1985). Bebi *et al.* (2003) concluded that spruce, *Picea engelmannii*, mortality to spruce beetle, *Dendroctonus rufipennis,* in Colorado, United States, did not increase the occurrence of subsequent fires. Péch (1993) found similar results for balsam fir, *Abies balsamea,* mortality to the spruce budworm, *Choristoneura fumiferana,* in eastern Canada. However, absence of subsequent fire in these cases may have reflected the rapid decomposition of spruce and fir litter (Bebi *et al.* 2003, Péch 1993).

III. SUMMARY

Herbivory, the feeding on living plant parts by animals, is a key ecosystem process that has widely recognized effects on primary production and on vegetation structure and composition. The effect of herbivory depends on herbivore feeding type and intensity. Different types of herbivory affect different tissues and the production, translocation, and accumulation of photosynthates to varying degrees.

A number of methods have been used to measure the intensity and effects of herbivory. The most common method for measuring intensity has been estimation of consumption rates by individual herbivores and extrapolation to population size. This method can be used to measure consumption by sap-sucking herbivores as well as folivores. A second method is measurement, by various means, of missing plant biomass. This method does not account for completely consumed (and unobserved) parts or for compensatory growth. Measurement of turnover of marked plant parts is the most accurate, but labor-intensive, method for estimating herbivory. Estimates of herbivory can differ by 2–5 times among methods, making standardization a key to comparison among ecosystems. Evaluating the effect of herbivory requires measurement of a variety of plant and ecosystem responses, not simply plant growth or productivity.

The intensity of herbivory varies widely, but a trend is apparent among ecosystem types. Herbivory generally is lowest (<2% reduction in primary production) in some forests and highest (most primary production consumed daily) in aquatic ecosystems. Insects are the primary herbivores in forest ecosystems and may account for the bulk of herbivory in grasslands, although vertebrate grazers are more conspicuous.

Herbivory has well-known effects on survival, productivity, and growth form of individual plants. However, the traditional view of herbivory as a negative effect on plants is being replaced by a view that recognizes more complex effects of variable intensity and timing. Moderate intensities of herbivory often stimulate production, through compensatory growth, and flowering, thereby increasing fitness. A given intensity of herbivory can have different effects at different times during the growing season or under different environmental conditions. Herbivory can affect the growth form of plants by terminating shoot growth and initiating branching and by affecting shoot-to-root ratios. Changes in survival, productivity, and growth of individual plant species affect vegetation structure and community dynamics. Herbivores often determine the geographic or habitat patterns of occurrence of plant species and facilitate successional transitions.

Few studies have addressed effects of insect herbivores on biogeochemical cycling or other abiotic conditions. However, herbivores affect, often dramatically, the turnover of plant nutrients to litter as plant fragments, feces and animal tissues, and nutrients leached from chewed surfaces. Folivory alters seasonal patterns of nutrient fluxes by transferring material prior to plant resorption of nutrients from senescing parts. Sap-sucking insects transfer copious amounts of labile carbohydrates (as honeydew) that stimulate growth and nutrient uptake by microbes. Herbivory also may affect climate and the likelihood and intensity of future disturbances. Reducing vegetation cover greatly affects the penetration of light, precipitation, and wind to the understory and soil, affecting soil warming and water content, relative humidity, erosion, transpiration, etc. Reduced vegetation biomass or litter accumulation affects abundance of fuel to support fire and affects water-holding capacity and vegetation demand for water during drought. Therefore, herbivory can influence ecosystem stability substantially (Chapter 15).

13

Pollination, Seed Predation, and Seed Dispersal

INSECTS AFFECT PLANT REPRODUCTION AND ASSOCIATED PROCESSES in a variety of ways. Direct and indirect effects of herbivores on plant production and allocation of resources to reproduction were described in Chapter 12. Pollination, seed predation, and seed dispersal are major processes by which insects (and other animals) affect plant reproduction and distribution. Pollinators control fertilization and reproductive rates for many plant species, especially in the tropics. In fact, some plant species depend on pollinators for successful reproduction and may disappear if their pollinators become rare or extinct (Powell and Powell 1987, Steffan-Dewenter and Tscharntke 1999). Seed predators consume seeds and thereby reduce plant reproductive efficiency but often move seeds to new locations and thereby contribute to plant dispersal. Many plant species depend on seed dispersers for successful movement of seeds to new habitats and may be vulnerable to disappearance of their dispersers (O'Dowd and Hay 1980, Schupp 1988, Witmer 1991). Pollinators and seed predators play important roles in seed production, seedling recruitment, and plant demography.

Insects are the major agents of pollination, seed predation, or seed dispersal in many ecosystems (Bawa 1990, Degen and Roubik 2004, Sallabanks and Courtney 1992). For example, Momose *et al.* (1998b) noted that for 270 plant species in a lowland dipterocarp forest in Sarawak, Malaysia, social bees were the primary pollinators for 44%, beetles for 24%, solitary bees for 19%, and birds and bats for 6%. Pollination and seed dispersal are among the most intricate mutualisms between animals and plants and have been studied widely from the perspective of co-evolution. Nevertheless, few studies have evaluated the effects of pollinators, seed predators, and seed dispersers on ecosystem processes, despite their importance to seedling recruitment and vegetation dynamics. Different functional groups of pollinators and seed-feeders affect seedling recruitment and vegetation dynamics in different ways.

I. TYPES AND PATTERNS OF POLLINATION

Plants exhibit a diversity of reproductive mechanisms. Many reproduce vegetatively, but this mechanism is limited largely to local reproduction. Genetic heterozygosity and colonization ability are increased by outcrossing. Although many plant species are capable of self-fertilization, a large percentage (a vast majority in some ecosystems) are self-incompatible, and many are dioecious (e.g., 20–30% of tropical tree species), with male and female floral structures separated among individual plants to preclude inbreeding (Bawa 1990, Momose *et al.* 1998a). Mechanisms for transporting pollen between individuals becomes increasingly critical for reproduction with increasing separation of male and female structures and increasing isolation of individual plants (Ghazoul and McLeish 2001, Regal 1982, Steffen-Dewenter and Tscharntke 1999).

Several mechanisms move pollen among flowering individuals. Pollen can be transferred between plants through abiotic and biotic mechanisms (Regal 1982). Pollen is transported abiotically by wind. Biotic transport involves insects (Fig. 13.1), birds, and bats. Insects are the major pollinators for a vast majority of plant species in the tropics (Bawa 1990), but the proportion of wind-pollinated plants increases toward the poles, reaching 80–100% at northernmost latitudes (Regal 1982). These mechanisms provide varying degrees of fertilization efficiency, depending on ecosystem conditions.

A. Pollinator Functional Groups

Functional groups of pollinators may be more or less restricted to groups of plants based on floral or habitat characteristics (Bawa 1990). A large number of pollinators are *generalists* with respect to plant species. This functional group includes many beetles, flies, thrips, etc. that forage on any floral resources available. *Specialist* pollinators often exploit particular floral characteristics that may exclude other pollinators. For example, nocturnally flowering plants with large flowers attract primarily bats, whereas plants with small flowers attract primarily moths. Long, bright-red flowers attract birds but are largely unattractive to insects (S. Johnson and Bond 1994). Such flowers often are narrow to hinder entry by bees and other insect pollinators (Heinrich 1979) but may nonetheless be pollinated by some insects (Roubik 1989). *Pollen feeders* feed primary on pollen (e.g., beetles and thrips) and are likely to transport pollen acquired during feeding, whereas others are primarily *nectar-feeders* (e.g., beetles, butterflies, moths, and flies) and transport pollen more coincidentally. In fact, many nectar feeders avoid

FIG. 13.1 Examples of pollinators. **A:** Honey bee, *Apis mellifera,* Louisiana, United States. **B:** Scarab beetle, Fushan Experimental Forest, Taiwan.

the reproductive organs, often by perforating the base of the flower to reach the nectar (Dedej and Delaplane 2004) or, in the case of ants, may reduce pollen viability (Peakall *et al.* 1987). Bees, especially *Apis* spp., primarily feed on pollen and nectar. Functional groupings also reflect attraction to floral odors. For example, dung-, fungus-, and carrion-feeding flies and beetles are the primary pollinators of plants that emit dung or carrion odors (Appanah 1990, Norman and Clayton 1986, Norman *et al.* 1992).

Ants frequently exploit floral resources but have little importance as pollinators. Peakall *et al.* (1987) suggested that antibiotic secretions produced by most ants, to inhibit infection by entomophagous fungi in a subterranean habitat, also inhibit germination of pollen. Ants lacking these secretions are known to function as pollinators.

Pollinator functional groups also have been distinguished on the basis of habitat preferences, such as vegetation stratum (Fig. 13.2). Appanah (1990) distinguished four groups of plant-pollinator associations in a tropical lowland dipterocarp forest in Malaysia. The *forest floor stratum* was characterized by low visibility and limited airflow. Floral rewards were small, reflecting low productivity of light-limited plants and low energy requirements of associated pollinators, and flowering times were extended, increasing the probability of pollination by infrequent visitors. The plant-pollinator association of this stratum was dominated largely by nonselective, low-energetic beetles, midges, and other flies. These pollinators were attracted over short distances by strong olfactory cues,

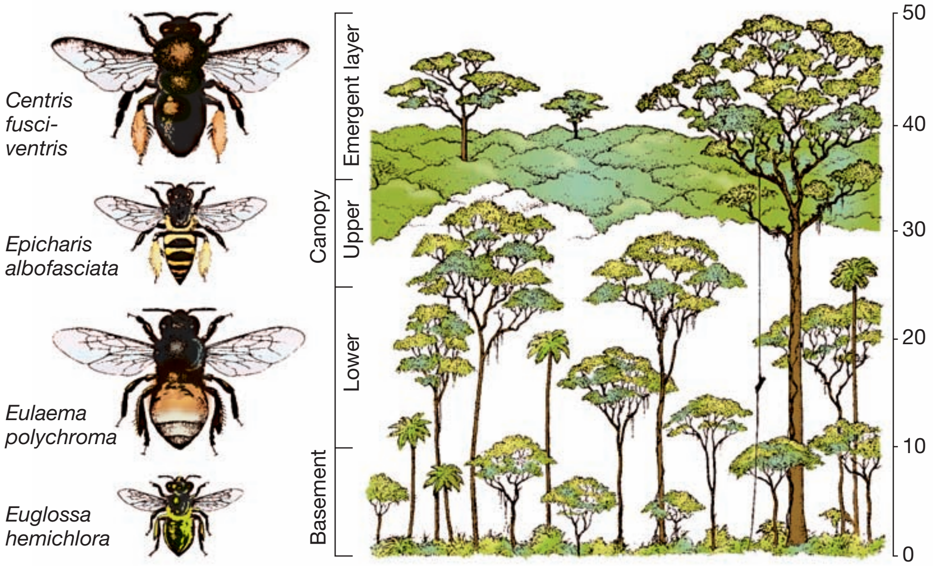


FIG. 13.2 Vertical stratification of pollinator species in a tropical rainforest. The two bee species above pollinate flowers in the upper canopy and the two species below pollinate flowers in the subcanopy. From Perry (1984) © George V. Kelvin/Scientific American.

often resembling dung or carrion, which have limited effective range. The *understory stratum* shared many of the environmental features of the forest floor. Plants in this stratum also offered limited visual cues and floral rewards and were pollinated by nonspecific trapliners (i.e., species that revisit particular plants along an established circuit; e.g., trigonid bees, solitary wasps, and butterflies). The *overstory stratum* generally was characterized by brightly colored flowers, held above the canopy to attract pollinators over a wide area, and brief, highly synchronized flowering within plant species. Dominant pollinators were *Apis dorsata* and trapliners such as carpenter bees, birds, and bats. Dipterocarps in the genera *Shorea, Hopea,* and *Dipterocarpus* formed a separate association based on tiny flowers with limited nectar rewards and nocturnal flowering. Thrips and other tiny, flower-feeding insects were the primary pollinators. By contrast, Sakai *et al.* (1999) observed that beetles (chrysomelids and curculionids), rather than thrips, were the primary pollinators of these tree species in Sarawak. Finally, some plant species representing various canopy positions were *cauliflorous* (i.e., they produced flowers along the trunk or main branches). These flowers usually were large, or small and clumped; pale colored; odiferous; and produced during a brief, highly synchronized period. Pollinators included understory and overstory insects, birds, and bats. Momose *et al.* (1998b) noted that long-distance pollinators tended to be less common in Malaysian forests than in Neotropical forests.

Roubik (1993) experimentally manipulated availability of floral resources from different canopy strata in tropical forests in Panama. Results indicated that the apparent fidelity of pollinator species to particular canopy strata reflected pollinator preferences for particular floral resources. Most pollinator species were attracted to their preferred floral resources regardless of their location in the canopy.

B. Measurement of Pollination

Pollination efficiency reflects the probability that pollen reaches a conspecific flower. A number of factors influence the efficiency of pollen transport between conspecific reproductive structures. The mechanism of pollen transport, proximity of conspecific plants, pollinator attraction to floral structures, adaptations for carrying pollen, fidelity, and thermodynamic constraints determine the probability that a flower will receive conspecific pollen.

Several methods have been used to measure pollinator activity and pollination efficiency. Observations of the type and frequency of floral visitors can provide a measure of pollinator activity (Aizen and Feinsinger 1994, Ghazoul and McLeish 2001, Sakai *et al.* 1999, Steffan-Dewenter and Tscharntke 1999, Steffan-Dewenter *et al.* 2001). Interception traps also can be used to collect insects visiting flowers (S. Johnson *et al.* 2004). The number of fertilized seeds per flower provides a measure of pollination for self-incompatible species (Steffan-Dewenter *et al.* 2001, S. Johnson *et al.* 2004). Kohn and Casper (1992) used electrophoresis to identify seeds containing alleles that did not occur in neighboring plants. G. White *et al.* (2002) used DNA (deoxyribonucleic acid) marker techniques to measure pollen transfer among trees, *Swietenia humilis,* in isolated fragments of tropical forest in Honduras.

Wind pollination is highly inefficient. The probability of successful pollen transfer by wind decreases as the cube of distance between plants (Moldenke 1976). However, plant investment in individual pollen grains is negligible so large numbers can be produced, increasing the cumulative probability that some will land on conspecific reproductive structures. Directed transport of pollen by animal pollinators increases efficiency to the extent that the pollinator visits a conspecific flower before the pollen is lost or contaminated with pollen from other plant species. Hence, animal-pollinated plant species may invest energy and nutrients in adaptations to improve the fidelity of the pollinator. These adaptations include nectar rewards to attract pollinators, floral and aromatic advertisements; floral structures that restrict the diversity of pollinators visiting the flowers, synchronized flowering among conspecific individuals, and divergence in time of flowering among plant species to reduce pollen contamination (Heinrich 1979).

Nectar rewards must be sufficient to compensate the pollinator for the foraging effort. For example, a greater nectar return is necessary to attract bees during cooler periods, when energy allocation to thermoregulation is high compared to warmer periods (Heinrich 1979). Heinrich (1979) noted that pollinator fidelity reflects offsetting adaptations. Plants invest the minimum amount of energy necessary to reward pollinators, but pollinators quickly learn to concentrate on flowers offering the greatest rewards. Individual plants in aggregations could attract bees and be pollinated even if they produced no nectar, provided that their neighbors produced nectar. The nonproducers should be able to invest more energy in growth and seed production. However, if these "cheaters" became too common, pollinators would switch to competing plant species that offered greater food rewards (Feinsinger 1983). A. Lewis (1993) suggested that floral characteristics may reflect advantages accruing to the plant when pollinators must make a substantial investment in learning to handle a flower, thereby becoming facultative specialists. Plant investment in attractants and rewards for pollinators represents an evolutionary tradeoff between growth and reproduction (Heinrich 1979) and may affect the ability of light- or resource-limited species to attract pollinators. Bawa (1990) reviewed studies that demonstrated long-distance pollen flow and outcrossing for tropical canopy trees but a high degree of inbreeding for many tropical herbs and shrubs.

Effects of pollination on plant seedling recruitment and ecosystem processes have been measured less frequently. Effects on seed production can be measured as the number of seeds produced when pollinators have access or are excluded from flowers (S. Johnson *et al.* 2004, Norman and Clayton 1986, Norman *et al.* 1992, Steffan-Dewenter and Tscharntke 1999, Steffan-Dewenter *et al.* 2001). Pollinator effects on ecosystem processes should reflect their direct influence on plant reproduction and indirect influence on vegetation dynamics.

C. Spatial and Temporal Patterns of Pollination

Pollination by insects is more prevalent in some types of ecosystems than in others. Pollination by animals is more common in angiosperm-dominated ecosystems than in gymnosperm-dominated ecosystems, but pollination by wind is energetically efficient for dominant species in grasslands and temperate forests.

The regularity with which conspecific plants occur in close proximity to each other largely determines their pollination mechanism. Long-lived species that dominate relatively simple ecosystems (i.e., grasslands and temperate forests) are pollinated primarily by wind. These plant species do not require efficient pollination or frequent reproduction to ensure population survival. Energetically inexpensive transport of pollen by wind provides sufficient pollination (and successful reproduction) so that energy need not be diverted to production of expensive nectar rewards and floral displays to advertise availability.

Directed transport of pollen by animals is critical to reproduction of plant species that are short-lived, are sparsely distributed, or occur in habitats with restricted airflow (Appanah 1990, Moldenke 1979, Regal 1982, Somanathan *et al.* 2004). In contrast to long-lived plants, short-lived plants have limited opportunities for future reproduction and, therefore, tend to depend on more efficient pollination to ensure seed production. Sparsely distributed plants and plants in areas of limited airflow cannot rely on inefficient transport of pollen by wind between distant or inaccessible individuals. Such species include early successional plants dominating ephemeral communities, widely spaced plants in harsh environments (e.g., deserts), scattered forbs in grasslands, subdominant trees, shrubs and herbs in temperate forests, and all (or most) plant species in tropical forests (S. Johnson *et al.* 2004, Momose *et al.* 1998b, Regal 1982). Regal (1982) reported that fewer than 6% of desert shrub species are wind pollinated. All of the 270 plant species in a lowland diperocarp forest in Sarawak, Malaysia, were animal pollinated, 90% by insects (Momose *et al.* 1998b).

Insects and other animal pollinators can transport pollen over considerable distances. Kohn and Casper (1992) documented gene flow among bee-pollinated buffalo gourds, *Cucurbita foetidissima,* over distances up to 0.7 km in New Mexico, United States. Somanathan *et al.* (2004) reported that carpenter bees, *Xylocopa tenuiscapa,* pollinated a Neotropical tree, *Heterophragma quadriloculare,* isolated from pollen sources by as much as 330 m, permitting reproduction by spatially isolated trees. G. White *et al.* (2002) identified sources of pollen reaching isolated *Swietenia humilis* trees and forest fragments in Honduras. A substantial proportion of pollen (25%) was transported over distances of >1.5 km, to more than 4.5 km between fragments. By contrast, a Neotropical shrub, *Lasiosiphon eriocephalus,* pollinated by a weakly flying nitidulid beetle, may be particularly vulnerable to isolation or fragmentation (Somanathan *et al.* 2004).

Roubik (1989) reviewed studies that distinguished seasonal patterns of pollinator activity. Primary pollinators usually were most active during periods of peak flowering. Heithaus (1979) reported that megachilid and anthophorid bees were most active during the dry season in Costa Rica, halictid bees during both wet and dry seasons, and andrenid and colletid bees during the wet season or during both seasons. Social pollinators (e.g., apid bees) require a sequence of floral resources throughout the year to support long-lived colonies and visit a succession of flowering plant species, whereas more ephemeral, solitary species with short life spans can be relatively more specialized on seasonal floral resources (S. Corbet 1997, Roubik 1989).

II. EFFECTS OF POLLINATION

Pollination contributes to genetic recombination and survival of plant species in heterogeneous environments. Many plants can reproduce vegetatively or by self-fertilization, but these mechanisms are not conducive to long-distance colonization or genetic recombination. Species survival and adaptation to changing environmental conditions requires outcrossing and environmental selection among diverse genotypes. Some long-lived perennials may endure adverse conditions and persist by vegetative reproduction until conditions favor outcrossing and seedling recruitment. Such windows of opportunity are unpredictable, requiring annual investment in flower and seed production (Archer and Pyke 1991).

Pollinator-facilitated reproduction is a key factor maintaining populations of ephemeral or sparsely distributed plant species. Obligate outcrossing plant species that depend on insect or vertebrate pollinators for pollination are vulnerable to loss of these mutualists. Maintenance of rare plant species or restoration of declining species depends to a large extent on protection or enhancement of associated pollinators (Archer and Pyke 1991, S. Corbet 1997). Norman and Clayton (1986) and Norman *et al.* (1992) found that pawpaws, *Asimina* spp., in Florida, United States, depended on beetle and fly pollinators attracted to yeasty floral odors. Self-pollinated flowers occasionally produced fruits, but only seeds from cross-pollinated flowers germinated.

Differential pollination and reproductive success among plant species affect vegetation dynamics. Plant species that maximize pollination efficiency and increase outcrossing via animal pollinators are able to persist as scattered individuals. However, pollination efficiency by insects is strongly affected by plant spacing. Momose *et al.* (1998a) found that pollination by thrips and consequent fruit and seed development of a small (<8 m height) tree species, *Popowia pisocarpa,* in Sarawak declined dramatically when distances between trees exceeded 5 m. Changes in pollinator abundances and pollination efficiency affect plant population dynamics and persistence in communities. Environmental changes that increase the distance between conspecific plants may threaten their survival, as shown in the following examples.

Steffan-Dewenter and Tscharntke (1999) examined the effects of plant isolation on pollination and seed production in replicate grasslands surrounded by intensively managed farmland. They established small experimental patches of two grassland species, *Sinapsis arvensis* and *Raphanus sativus,* at increasing distances from the grassland boundaries and found that the number and diversity of bees visiting flowers, and seed production, declined with increasing isolation (Fig. 13.3). Number of seeds per plant was reduced by 50% at 260 m from the nearest grassland for *R. sativus* and at 1000 m for *S. arvensis.*

Changes in pollinator abundance, such as those resulting from ecosystem fragmentation, can affect plant reproduction and gene flow (Bawa 1990, Didham

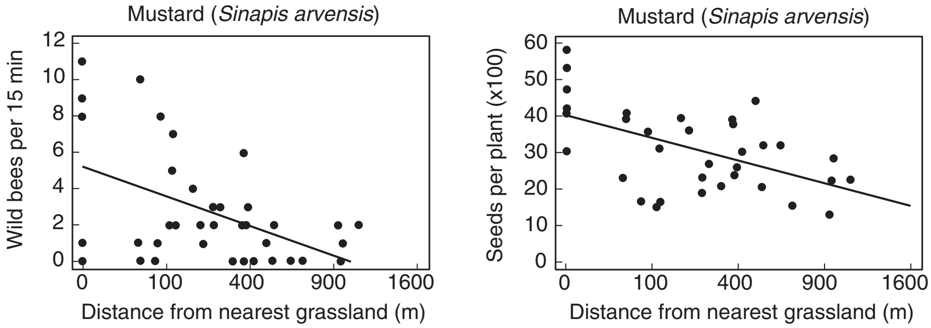


FIG. 13.3 Relationship between the plant distance from the nearest chalk grassland and abundance of pollinating bees per 15 minutes (*left*) and number of seeds per plant (*right*). The regression lines are significant at $P < 0.003$. From Steffan-Dewenter and Tscharntke (1999) with permission from Elsevier. Please see extended permission list pg 572.

et al. 1996). Powell and Powell (1987) compared attraction of male euglossine bees to floral chemical baits in forest fragments in Brazil. Abundance and species composition did not differ among sites prior to fragmentation. However, after fragmentation, visitation rates for most species were correlated to fragment size, and the bee species trapped in clearings differed from the species trapped in forests (Fig. 13.4). Powell and Powell (1987) concluded that the reduced abundance and activity of particular pollinators in fragmented forests threatened the viability of their orchid hosts. Aizen and Feinsinger (1994) compared pollinator visitation among replicated blocks containing continuous forest and large (>2.2 ha) and small (<1 ha) fragments in subtropical dry forest in northwestern Argentina. The diversity and visitation frequency of native pollinators decreased significantly, and the visitation frequency of exotic honey bees, *Apis mellifera,* increased significantly with decreasing fragment size (Fig. 13.5). Fragments supported fewer bee species than did continuous forests. Although honey bees from the surrounding agricultural matrix replaced most of the lost visitation by native pollinators, some plant species could be threatened by loss or reduced specificity of pollinators.

Pollination also contributes to production of fruits and seeds that support associated food webs. Many animal species depend on fruit and seed production, at least seasonally (see later in this chapter). Hence, pollination of fruiting plants has consequences not only for plant reproduction but also for the survival of frugivores and seed predators (Bawa 1990).

Pollinators can affect ecosystem energy and nutrient fluxes. Roubik (1989) calculated the effects of social bees on energy and nitrogen budgets of tropical forests in Central America. He estimated that 600 colonies km^{-2} harvested 1.4×10^{7} kJ year^{-1} and disposed of an equivalent energy value represented by dead bees scattered on the ground within a few dozen meters of each nest. This value exceeded estimates of energy fixed annually by primary producers, indicating that the energetics of flowering are greatly underestimated

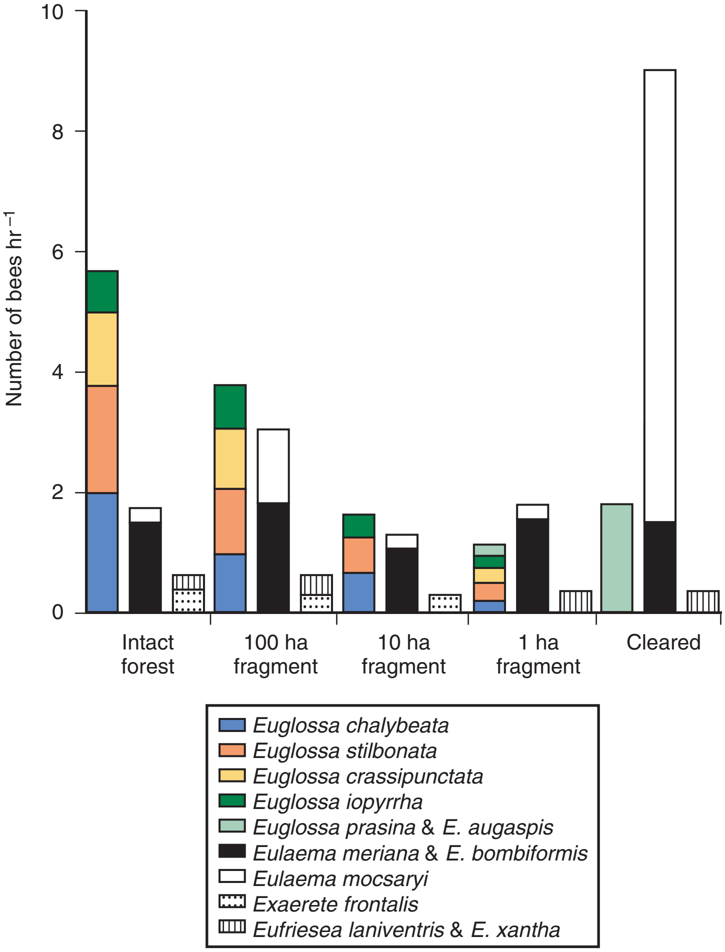
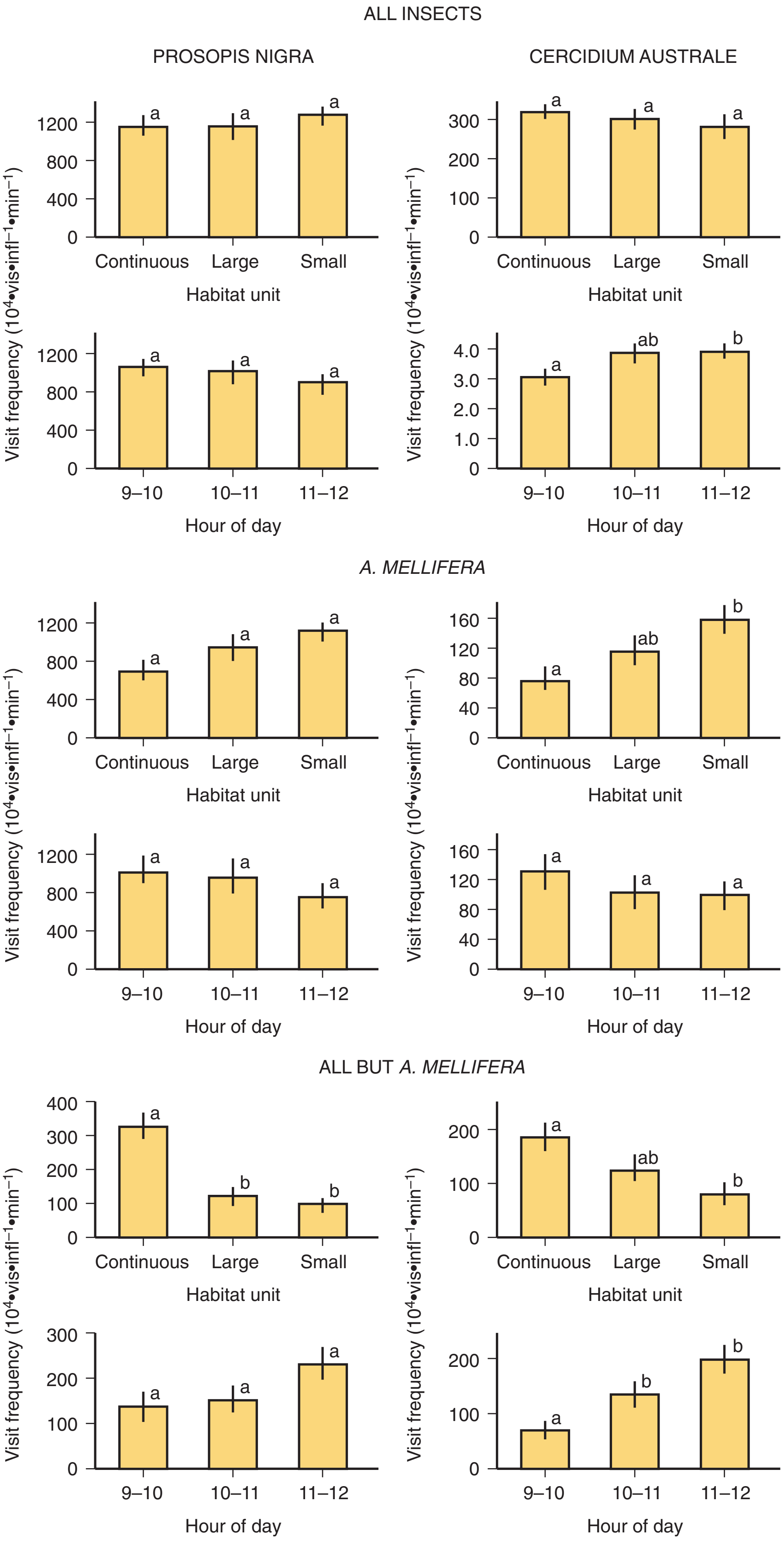


FIG. 13.4 Rates of visitation by male euglossine bees at chemical baits in intact forest, forest fragments of varying size (100 ha, 10 ha, and 1 ha), and recently deforested (500 ha). Modified from Powell and Powell (1987) with permission from the Association for Tropical Biology.

(Roubik 1989). The 600 colonies also distributed about 1800 kg trash (pupal exuviae and feces) ha^{-1} year^{-1}. At 4% nitrogen content, this represents a flux of 72 kg ha^{-1} year^{-1} or about 1% of above-ground nitrogen in biomass. Pollinator effects on community structure also should affect ecosystem processes. These effects warrant further study.

FIG. 13.5 Rates of visitation by all pollinating insects, exotic honey bees (*Apis mellifera)* alone, and native pollinators alone on flowers of two plant species by treatment (continuous forest, and large [2.2 ha] and small [1 ha] fragments) and by time of day in Argentina. Vertical lines represent standard errors; bars under the same letter do not differ at $P < 0.05$. From Aizen and Feinsinger (1994) with permission from the Ecological Society of America.


ALL INSECTS
PROSOPIS NIGRA
CERCIDIUM AUSTRALE
Visit frequency (10⁴•vis•infl⁻¹•min⁻¹)
0
400
800
1200
a
a
a
Continuous
Large
Small
Habitat unit
0
100
200
300
a
a
a
a
a
a
9–10
10–11
11–12
Hour of day
0
1.0
2.0
3.0
4.0
a
ab
b
A. MELLIFERA
a
a
a
0
40
80
120
160
a
ab
b
a
a
a
a
a
a
ALL BUT A. MELLIFERA
0
100
200
300
400
a
b
b
0
100
200
a
ab
b
a
a
a
a
b
b

III. TYPES AND PATTERNS OF SEED PREDATION AND DISPERSAL

The fate of seeds is critical to plant reproduction. A variety of animals feed exclusively or facultatively on fruits or seeds, limiting potential germination and seedling recruitment. Many animals, especially frugivores, facilitate seed dispersal. Dispersal of seeds is necessary for colonization of new habitats and for escape from high mortality near parent plants, but relatively few studies have measured the advantages of seed dispersal to plant fitness (Howe and Smallwood 1982). In contrast to pollination, effective seed dispersal relies less on disperser specialization than on movement to suitable habitat (Wheelwright and Orians 1982). These mechanisms confer varying degrees of dispersal efficiency and advantages for seedling growth, depending on ecosystem conditions.

A. Seed Predator and Disperser Functional Groups

Fruits and seeds are highly nutritive food resources as a consequence of plant provision for germination and, often, attraction of dispersal agents. A wide variety of animals feed on fruits or seeds. For example, Turgeon *et al.* (1994) reported that more than 400 species of insects, representing seven orders, feed on conifer cones, seeds, or both. Some species are obligate fruit- or seed-feeders, whereas others feed primarily on other resources but exploit fruits, seeds, or both when available.

Seed dispersal can be accomplished through both abiotic and biotic mechanisms. Abiotic dispersal involves wind and water; biotic dispersal involves autogenic mechanisms, such as explosive fruits, and various animal agents, including insects, fish, reptiles, birds, and mammals. Dispersal by animals usually is a consequence of frugivory or seed predation, but some species acquire seeds or spores through external attachment by various kinds of clinging devices (e.g., sticky material or barbed spines). Seeds of a majority of plant species are dispersed by animals in many ecosystems (Howe and Smallwood 1982).

Seed predator and seed disperser functional groups can be distinguished on the basis of consumption of fruits or seeds versus transport of seeds. *Frugivores* feed on fleshy fruits and may terminate fruit or seed development (Sallabanks and Courtney 1992), but many vertebrate frugivores (including fish, reptiles, birds, and mammals) consume entire fruits and disperse seeds that are adapted to survive passage through the digestive tract (Crawley 1989, de Souza-Stevaux *et al.* 1994, M. Horn 1997, Sallabanks and Courtney 1992, Temple 1977). *Seed predators* include a number of insect, bird, and rodent species that consume seeds where found. Some seed predators eat the entire seed (e.g., vertebrates and ants), but others penetrate the seed coat and consume only the endosperm (e.g., seed bugs, Lygaeidae and Coreidae, and weevils, Curculionidae) or develop and feed within the seed (e.g., seed wasps, Torymidae, and seed maggots, Anthomyiidae) (J. Brown *et al.* 1979, Crawley 1989, Louda *et al.* 1990b, Schowalter 1993, Turgeon *et al.* 1994). *Seed cachers* eat some seeds and move others from their original location to storage locations. Although ants and rodents are best known for caching seeds (J. Brown *et al.* 1979), at least one carabid beetle, *Synuchus impunctatous,* caches seeds of *Melampyrum* in hiding places after consuming the caruncle at the end of the seed (Manley 1971). *Seed vectors* include primarily vertebrates that carry seeds adapted to stick to fur or feathers. Insects generally are too small to transport seeds in this way but often transmit spores of microorganisms adapted to adhere to insect exoskeletons or pass through insect digestive systems.

These functional groups can be subdivided on the basis of predispersal or postdispersal seed predation, seed size, etc. Predispersal frugivores and seed predators feed on the concentrated fruits and seeds developing on the parent plant, whereas postdispersal frugivores and seed predators must locate scattered fruits and seeds that have fallen to the ground. Rodents and birds usually exploit larger seeds than do insects, and species within taxonomic groups also partition seeds on the basis of size (e.g., J. Brown *et al.* 1979, Davidson *et al.* 1984, Whitford 1978). Vertebrates are more likely to disperse seeds from consumed fruits than are insects, which (because of their small size) usually feed on portions of fruits and on or in seeds. However, dung beetles and ants may be important secondary dispersers, redistributing seeds from animal dung (Andresen 2002, Martínez-Mota *et al.* 2004). Insects, especially ants, are more likely to disperse small seeds, particularly of plant species adapted for dispersal by ants (myrmecochory).

B. Measurement of Seed Predation and Dispersal

A number of factors influence rates of seed predation and dispersal. The extent of seed mortality, mechanism of seed transport, distance moved from the parent plant, attraction of particular dispersal agents, and thermodynamic constraints determine the probability that seeds will survive and be moved to suitable or distant locations. Pollinators and seed predators can have opposing effects on seed production. Steffen-Dewenter *et al.* (2001) reported that pollinator activity decreased, but seed predation increased, on experimental *Centaurea jacea* plants, with distance from seminatural habitats in an agricultural landscape in Germany.

Several methods have been used to measure seed predation and dispersal. Predispersal seed predation can be measured by marking fruits or seeds on the plant and observing their fate, using a life table approach (see Chapter 5). Mature fruits and seeds can be collected for emergence of seed predators (Steffan-Dewenter *et al.* 2001) or dissected or radiographed for identity and number of internal seed predators or evidence of endosperm digestion by heteropterans (e.g., Schowalter 1993). Seed-piercing Heteroptera may leave detectable pectinases or stylet sheaths on the seed coat of consumed seeds (Campbell and Shea 1990). Postdispersal seed predation can be measured by placing marked seeds on the ground and measuring rate of disappearance (C. Chapman and Chapman 1996, Heithaus 1981, O'Dowd and Hay 1980, Schupp 1988). Seeds marked with tracers can be identified in caches or fecal material for assessment of seed dispersal rate (e.g., O'Dowd and Hay 1980).

Seed predators are capable of consuming or destroying virtually the entire production of viable seed of a given plant species in some years (Coe and Coe 1987, Ehrlén 1996, Robertson *et al.* 1990, Schowalter 1993, Turgeon *et al.* 1994). The intensity of seed predation depends to a large extent on seed availability. Seed predators focus on the largest or most concentrated seed resources (Ehrlén 1996). During years of poor seed production, most or all seeds may be consumed, whereas during years of abundant seed production, predator satiation enables many seeds to survive (Schowalter 1993, Turgeon *et al.* 1994). Long-lived plant species need produce few offspring over time to balance mortality. Hence, many tree species produce abundant seed only once every several years. Years of abundant seed production are known as mast years. Poor seed production during intervening years reduces seed predator populations and increases efficiency of seed production during mast years (Fig. 13.6).

Insects generally are more important predispersal seed predators than are vertebrates, but vertebrates are more important postdispersal seed predators (Crawley 1989, Davidson *et al.* 1984, Louda *et al.* 1990b, Schupp 1988). Predispersal seed predators greatly reduce seed production efficiency and reduce the number of seeds available for postdispersal seed predators and dispersal. K. Christensen and Whitham (1991) reported that seed-dispersing birds avoided foraging in pinyon pine trees in which the stem- and cone-boring moth, *Dioryctria albovitella,* had inhibited cone development and increased cone mortality. At the same time, frugivores and postdispersal seed predators consume colonized seeds and can significantly reduce populations of predispersal seed predators (Coe and Coe 1987, Herrera 1989). Sallabanks and Courtney

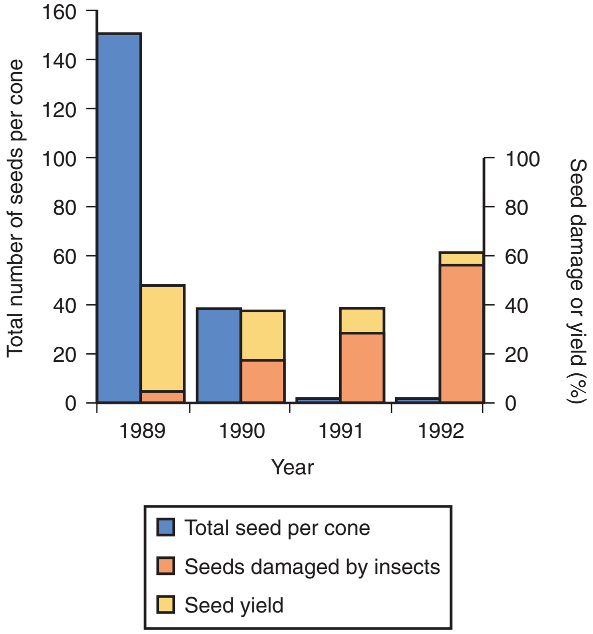


FIG. 13.6 Relationship between total seed produced, seed loss to insects, and seed yield in a Douglas fir seed orchard in western Oregon. Data from Schowalter (1993).

(1992) suggested that seed predators and dispersers often may exert opposing selection pressures on temporal and spatial patterns of fruit and seed production.

Seed dispersal is an important mechanism for plant colonization of new sites. However, dispersal also may increase seed and seedling survival. Schupp (1988) reported that vertebrate seed predators limited seed survival under the parent tree to 15% of marked seeds but that dispersal distances of only 5 m significantly increased seed survival to nearly 40% over a 7-month period (Fig. 13.7). C. Chapman and Chapman (1996) compared fruit and seed disappearance and survival of seeds remaining under the parent canopy for six tree species in a tropical forest in Uganda. Three of the six species showed higher rates of seed removal at locations away from the parent canopy compared to locations under the parent canopy, whereas the other three species showed no difference in seed removal between locations. However, for two of the latter species, survival of transplanted seedlings was much higher under conspecific canopies than at locations away from conspecifics, but subsequent herbivory tended to be higher on seedlings under conspecific trees. Fruits not harvested by dispersers usually rot on the ground, destroying the seeds within (Asquith *et al.* 1999, Janzen and Martin 1982). Ants often play a critical role in seedling survival and germination under parent trees by foraging on fruit, cleaning seeds, and dispersing seeds to ant nests (Oliveira *et al.* 1995, Passos and Oliveira 2003). Seeds not cleaned by ants succumb to decay. These results indicate that seed dispersal to suitable sites represents various tradeoffs. Nevertheless, the efficiency with which seeds reach favorable sites is critical to plant population dynamics.

Seeds transported by wind or water often have low dispersal efficiency, for which plants must compensate by producing large numbers of seeds. Animals are

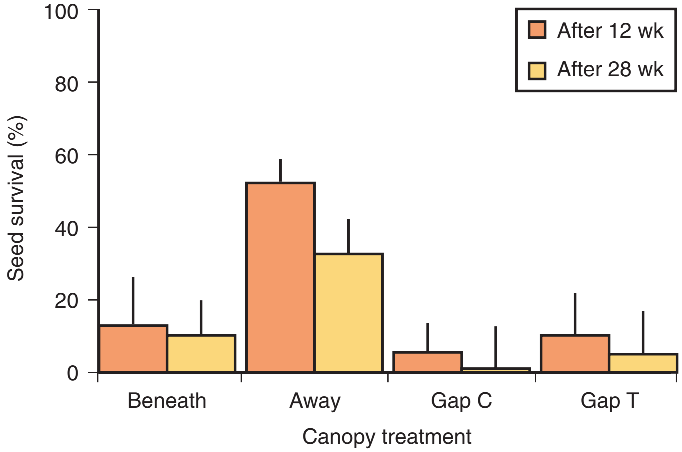


FIG. 13.7 Survival of *Faramea occidentalis* seeds beneath fruiting parent trees (*Beneath*), away from parent trees (*Away;* 5 m from crown perimeter of nearest fruiting adult), and within the canopy (*Gap C*) and trunk (*Gap T*) zones of treefall gaps on Barro Colorado, Panama. Survival of seed was significantly ($P < 0.05$) higher 5 m from parent trees than beneath parent trees or in treefall gaps. Data from Schupp (1988).

presumed to be more efficient dispersal agents, but this may not always be accurate. Seeds drop from animal vectors with no more likelihood of landing on suitable germination sites than do seeds deposited by wind or water, unless animal dens or habitats provide suitable germination sites. However, the direction of animal movement is more variable than that of wind or water. Birds, in particular, quickly cover large areas, but local seed redistribution by ants also can significantly affect plant demographies (Gorb and Gorb 2003, O'Dowd and Hay 1980). A number of plant species are specifically adapted for seed dispersal by animals. Myrmecochorous species produce a lipid-rich elaiosome to attract ants, which move seeds variable distances, depending on whether the elaiosome is removed prior to or during transport or at the nest (Fig. 13.8; Gorb and Gorb 2003). Some species with large seeds or thick seed coats may show reduced dispersal or germination ability where movement by animals or seed scarification is prevented (Culver and Beattie 1980, Oberrath and Böhning-Gaese 2002, Temple 1977). However, many seeds are dispersed more passively by various animals, including secondary dispersers such as dung beetles that redistribute frugivore dung (Fig. 13.9).

Seed storage underground by ants and rodents may move seeds to sites of better soil conditions or reduce vulnerability to further predation. A number of studies have demonstrated that seedlings germinating in ant nests are larger and have higher survival rates than do seedlings emerging elsewhere (A. Andersen 1988, Bennett and Krebs 1987, Culver and Beattie 1980, Rissing 1986, D. Wagner 1997). Ant nests may or may not enrich surrounding soils (Horvitz and Schemske 1986, Westoby *et al.* 1991; see Chapter 14). Soil from ant nests often has significantly higher concentrations of nitrate, ammonium, phosphorus, and water and higher nitrogen mineralization rates than does soil away from nests (A. Andersen 1988, Culver and Beattie 1983, Herzog *et al.* 1976, Holdo and McDowell 2004, Lesica and Konnowski 1998, Mahaney *et al.* 1999, D. Wagner 1997, D. Wagner *et al.* 1997). However, Rice and Westoby (1986), Hughes (1990), and Gorb and Gorb (2003) found that myrmecochorous plants do not necessarily show distribution patterns associated with soil fertility or with ant nests. Gorb and Gorb (2003) found that foraging *Formica polyctena* transported myrmecochorous seeds to territorial borders after removing the elaiosome, thereby distributing seeds widely, but non-myrmecochorous seeds were transported to nests, where they remained, leading to increased competition between plants that grew on the mound.

Plants may benefit from seed deposition at suitable depths for germination or protected from intense predation by vertebrates (Cowling *et al.* 1994). Shea *et al.* (1979) found that germination of serotinous seeds of several legume species, in Western Australia, was enhanced by seed redistribution by ants to depths that were heated sufficiently but protected from higher surface temperatures during high-intensity autumn fires. O'Dowd and Hay (1980) reported that transport of diaspores of *Datura discolor* by ants, to nests averaging only 2.3 m from the nearest plant, reduced seed predation by desert rodents from 25–43% of seeds in dishes under parent plants to <1% of seeds in dishes near ant nests. Heithaus (1981) found that when seed dispersal by ants was experimentally prevented, rodents removed 70–84% of *Asarum canadense* and *Sanguinaria canadensis* seeds, compared to 13–43% of seeds lost when ants were present. Fur-

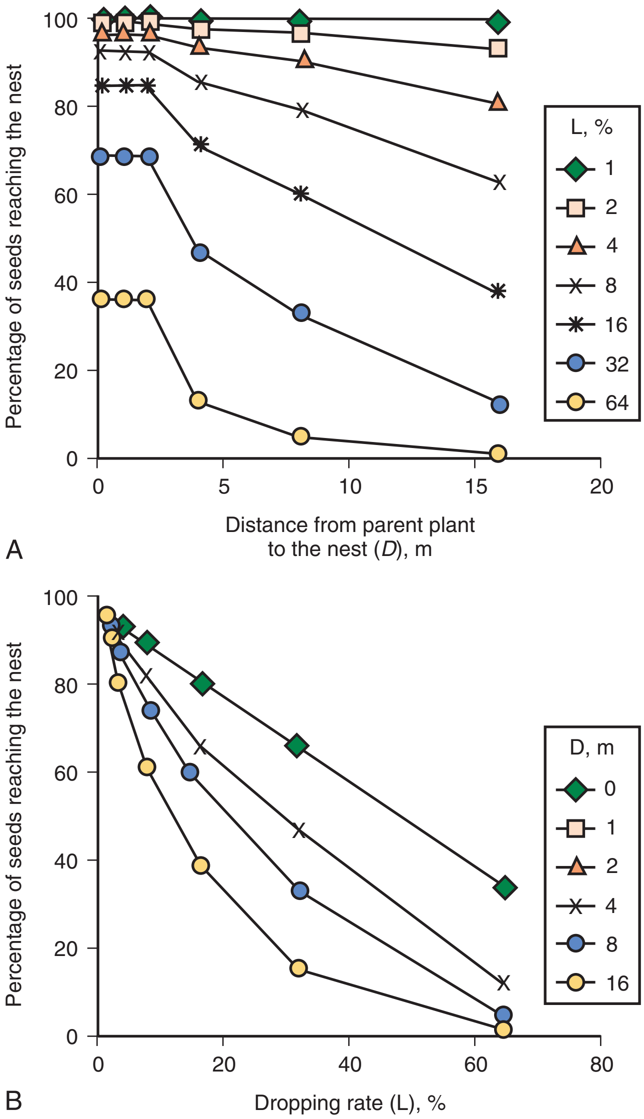


FIG. 13.8 Relationship between seed number transported to ant nests and distance from the parent plant to the nest for given diaspore dropping rates (*A*) and relationship between seed number transported to nests and dropping rate of diaspores for given distances from the nest (*B*). From Gorb and Gorb (2003) with permission from Kluwer Academic Publishers. Please see extended permission list pg 572.

thermore, laboratory experiments demonstrated that rodents located buried seeds less frequently than seeds on the surface and consumed buried seeds less often when elaiosomes were removed, as done by ants. Hughes (1990) reported that changes in nest structure, indicated by relocation of nest entrances, may provide refuges for seeds remaining in abandoned portions of nests and reduce seedling competition by preventing long-term concentration of seeds in localized sections of nests.

FIG. 13.9 Dung beetles represent secondary dispersers of seeds in vertebrate dung.

C. Spatial and Temporal Patterns of Seed Predation and Dispersal

Few studies have compared seed predation and dispersal among ecosystems. Different agents dominate these processes in different ecosystems (Moll and McKenzie 1994). For example, dominant plant species in temperate, especially arid, ecosystems frequently have wind-dispersed seed, whereas plant species on oceanic islands often are water-dispersed (Howe and Smallwood 1982). Howe and Smallwood (1982) concluded that consistently windy ecosystems promote wind-driven dispersal, whereas more mesic conditions promote animal-driven dispersal. Old World deserts have relatively few (<5%) animal-dispersed plant species (Howe and Smallwood 1982). More than 60% of temperate and tropical forest plant species are dispersed by animals (Howe and Smallwood 1982). A variety of large vertebrate herbivores are important frugivores and seed dispersers in temperate and tropical ecosystems (e.g., Janzen and Martin 1982). Fruits and seeds in seasonally flooded tropical forests often are dispersed by fish during periods of inundation (de Souza-Stevaux *et al.* 1994, M. Horn 1997, Howe and Smallwood 1982). Bats and primates are more important frugivores and seed dispersers in tropical forests than in temperate ecosystems. Insects are ubiquitous frugivores and seed predators but may be more important dispersers in grassland and desert ecosystems, where transport to ant nests may be critical to protection of seeds from vertebrate seed predators, from competition, and from fire (e.g., Louda *et al.* 1990b, Rice and Westoby 1986).

Rice and Westoby (1986), Rissing (1986), and Westoby *et al.* (1991) discussed a number of potential factors affecting differences in the incidence of ant-dispersed seeds among biogeographic regions. Myrmecochory appears to be more prevalent in Australia and South Africa than in other regions. One hypothesis is that smaller plants (characteristic of arid biomes) generally are more likely to be ant-dispersed than are larger plants. A second hypothesis is that the relatively infertile soils of Australia and South Africa preclude nutrient allocation to fruit production, forcing plants to adapt to seed dispersal by ants rather than vertebrates. Finally, Australia and South Africa lack the large harvester ants (e.g., *Pogonomyrmex* spp., *Messor* spp., and *Veromessor* spp.) common in arid regions of North America and Eurasia. These ants consume relatively large seeds, limiting the value of an elaiosome as a food reward for seed dispersal.

IV. EFFECTS OF SEED PREDATION AND DISPERSAL

Seed predators and dispersers influence plant population dynamics and community structure by affecting both seed survival and seedling recruitment. Robertson *et al.* (1990) reported that predispersal seed predation rates varied widely among mangrove species at study sites in northeastern Australia. Three species (*Ceriops australis, C. tagal,* and *Rhizophora apiculata)* had fewer than 10% of seeds damaged by insects, whereas six species (*Avicennia marina, Bruguiera gymnorrhiza, B. parviflora, Heritiera littoralis, Xylocarpus australasicus,* and *X. granatum)* consistently had >40% of seeds damaged. These mangrove species also showed variation in survival and growth rates (height and diameter) of seedlings from insect-damaged seeds. Ehrlén (1996) reported a significant positive correlation between the change in population growth rate and the reproductive value of seeds, as reduced by seed predation, indicating that survival of seeds and seedlings is the most important aspect of seed predator effects on plant population growth.

Postdispersal seed predators similarly affect the survival and growth of seeds and seedlings. Seeds selected for storage in ant nests or refuse piles often show increased survival and seedling growth, relative to seeds in control sites (A. Andersen 1988, Culver and Beattie 1980, Hughes 1990, Rissing 1986). Enhanced seedling growth on ant nests may reflect the higher nutrient concentrations (A. Andersen 1988, Culver and Beattie 1983, Herzog *et al.* 1976, Holdo and McDowell 2004, Mahaney *et al.* 1999, D. Wagner 1997, D. Wagner *et al.* 1997), greater water-holding capacity (Jonkman 1978, D. Wagner 1997) of ant nests, or protection from vertebrate seed predators or fire (Louda *et al.* 1990b, Rice and Westoby 1986).

The composition of the granivore community affects plant community development. R. Inouye *et al.* (1980) reported that exclusion of granivorous rodents or ants altered densities and community composition of annual plant species (Table 13.1). Rodents preyed selectively on large-seeded species (e.g., *Erodium* spp. and *Lotus humistratus)*. In plots from which rodents were excluded, these species increased to dominate vegetative biomass and replace small-seeded plant

TABLE 13.1 Effects of removal of ants, rodents, or both on densities of certain annual plant species, all plants, plant biomass, and two measures of species diversity. Values given are ratios of treatment to control (+Rodents +Ants) means. Numbers in parentheses are mean values for unthinned plots except for plant biomass and the two measures of diversity, which are for control plots. Statistical analysis was by ANOVA.

	+Rodents +Ants	**+Rodents –Ants**	**–Rodents +Ants**	**–Rodents –Ants**	**Effects of removal of**	
					Rodents	**Ants**
Initial Census 29 January 1977						
1. Large plants	1.00 (35.8)	0.98	2.08	2.35	Increase[b]	NS
2. Small plants	1.00 (292.5)	3.30	3.32	3.17	NS	Increase[b]
Final Census 2 April 1977						
3. *Erodium cicutarium* (seed mass = 1.6 mg)	1.00 (1.8)	1.83	7.03	16.11	Increase[b]	NS
4. *E. texanum* (seed mass = 1.6 mg)	1.00 (0.6)	0.88	2.07	0.78	Increase[a]	NS
5. *Euphorbia polycarpa* (seed mass = 0.2 mg)	1.00 (0.6)	2.00	0.14	0.29	Decrease[a]	NS
6. *Filago californica* (seed mass = 0.04 mg)	1.00 (142.1)	1.90	1.43	2.59	NS	Increase[a]
7. *Lotus humistratus* (seed mass = 1.5 mg)	1.00 (11.4)	1.14	2.43	5.22	Increase[b]	NS
8. All plants	1.00 (209.6)	1.35	1.34	1.94	Increase[a]	Increase[b]
9. Dry mass (all species)	1.00 (5.8)	1.07	2.09	2.17	Increase[b]	NS
10. Species diversity (H')	1.00 (2.78)	0.73	0.99	0.89	NS	Decrease[a]
11. Species evenness (E)	1.00 (0.53)	0.77	1.99	1.04	NS	Decrease[a]

ANOVA, analysis of variance; NS, not significant.

[a] Significant at $P < 0.05$.

[b] Significant at $P < 0.01$.

Reproduced from R. Inouye *et al.* (1980) with permission from the Ecological Society of America.

species, especially *Euphorbia polycarpa.* Ants preyed most intensively on the most abundant plant species (*Filago californica*). When ants were excluded, this small-seeded composite became numerically dominant and reduced species diversity.

Many plant species have become dependent on animal mutualists for seed dispersal. Seed and seedling survival for some species depends on distance from parent plants, under which seed predation may be concentrated (O'Dowd and Hay 1980, Schupp 1988). As found by Powell and Powell (1987) and Steffan-Dewenter and Tscharntke (1999) for pollinators (see earlier in this chapter), decline in abundance of seed dispersal agents may threaten persistence of some plant species.

Plant species adapted for dispersal by vertebrates often have hardened seed coats to survive gut passage and may require scarification during passage through the digestive systems before germination is possible. Temple (1977) noted the coincidence between the age (300–400 years) of the last naturally regenerated tambalacoque trees, *Sideroxylon sessiliflorum* (= *Calvaria major)* and the disappearance of the dodo in 1680 on the South Pacific island of Mauritanius. When *S. sessiliflorum* seeds were force fed to turkeys (approximately the size of the dodo), the seed coats were sufficiently abraded during gut passage to permit germination, demonstrating a potential role of the dodo in dispersal and survival of this once-dominant tree. Although the primacy of the dodo's role in *S. sessiliflorum* survival has been challenged (e.g., Witmer 1991), it appears that *S. sessiliflorum* and other plant species have suffered from disappearance of seed-dispersing animals from Mauritanius. Janzen and Martin (1982) suggested that a number of tropical plants may show reduced seed dispersal as a result of the Pleistocene extinction of the large mammalian fauna that likely fed on their fruits and dispersed seeds. In any event, many large-fruited species experience high seed mortality in fruits rotting under trees in the absence of effective dispersal (Asquith *et al.* 1999, Janzen and Martin 1982, Oliveira *et al.* 1995). Disappearance of native ant seed dispersers as a result of habitat fragmentation or competition from invasive ant species (e.g., A. Suarez *et al.* 1998) similarly may threaten the survival of ant-dispersed plant species. However, seed dispersers also have been shown to facilitate the spread of exotic plant species (J. M. B. Smith 1989).

The effects of seed predation and dispersal on nutrient cycling or other ecosystem processes have not been studied. However, these organisms affect the movement of nutrients in fruits and seeds. By dispersing fruits and seeds, frugivores in particular remove the large energy and nutrient pools in fruits from under parent trees and distribute these over a large area. Furthermore, as for herbivores and pollinators, seed predators and dispersers affect the spatial distribution of various plant species that differentially control nutrient fluxes.

V. SUMMARY

Insects are the major agents of pollination, seed predation, or seed dispersal in many ecosystems. Although few studies have evaluated the effects of pollinators, seed predators, and seed dispersers on ecosystem processes, these organisms often are critical to seedling recruitment and vegetation dynamics that affect other ecosystem processes.

Pollination is an important means of increasing genetic heterogeneity and improving plant fitness. Pollination can be accomplished by abiotic (wind) or biotic (insects, birds, and bats) agents. Wind pollination is inefficient but sufficiently effective for species that dominate temperate ecosystems. However, animal agents increase pollination efficiency for more isolated plants and are critical to survival of many plant species that usually occur as widely scattered individuals, especially in deserts and tropical forests. Pollinator functional groups can be distinguished on the basis of their degree of specialization on particular floral resources.

Seed predators often consume the entire reproductive effort of host plants. Predispersal seed predators usually focus on concentrated seed resources on the parent plants, whereas postdispersal seed predators must locate more scattered seed resources on the ground. Insects are more important predispersal seed predators, but vertebrates are more important postdispersal seed predators in most ecosystems.

Seed dispersal is critical to plant species survival both because new habitats can be colonized and because seed relocation often improves seed and seedling survival. Seeds can be dispersed by abiotic (wind and water) or biotic (insect and vertebrate) agents. Animals can increase dispersal efficiency by moving seeds to more suitable germination sites, especially if seeds are buried. Ants, in particular, can increase seed survival and seedling growth by relocating seeds to nests, where seeds are protected from further predation, from suboptimal surface conditions, and from competition with parent plants. Ant nests also may provide more suitable soil conditions for germination and growth. Some seeds require scarification of hard seed coats and must pass through vertebrate digestive systems before germination can occur.

Both pollination and seed dispersal affect plant population and community dynamics. Differential pollination, seed predation, and seed dispersal efficiencies among plant species affect seedling recruitment and growth. Survival of some plant species depends on sufficient abundance of pollinators, seed dispersers, or both. However, research should address the extent to which pollinators, seed predators, and seed dispersers affect ecosystem processes.

14

Decomposition and Pedogenesis

DECOMPOSITION IS THE BREAKDOWN OF DEAD ORGANIC MATTER THAT eventually results in release of CO_2, other organic trace gases, water, mineral nutrients, and energy. Pedogenesis (soil development) largely reflects the activities of animals that mix organic matter with mineral soil. These two processes contribute greatly to the capacity of a site to support primary production. Accumulated organic litter represents a major pool of energy and nutrients in many ecosystems. Carbon and other nutrients released through decomposition can be acquired by plants or microbes or returned to abiotic pools (see Chapter 11). Incorporation of decay-resistant organic matter and nutrients into soil increases fertility, aeration, and water-holding capacity. Release of CO_2, CH_4, and other trace gases affects atmospheric conditions and global climate.

Decomposition can be categorized into four component processes: *photooxidation,* abiotic catabolism resulting from exposure to solar radiation; *leaching,* the loss of soluble materials as a result of percolation of water through material; *comminution,* the fragmentation of organic litter, largely as a result of detritivory; and *mineralization,* the catabolism of organic molecules by microorganisms. Vossbrinck *et al.* (1979) found that when arthropods and microbes were excluded, detritus lost only 5% mass, due entirely to leaching or photooxidation. A variety of macroarthropods, mesoarthropods, and microarthropods are the primary detritivores in most ecosystems. The feeding and burrowing activities of many animals, including ants, termites, and other arthropods, redistribute and mix soil and organic material. Burrowing also increases soil porosity, thereby increasing aeration and water-holding capacity.

The effects of arthropod detritivores and burrowers on decomposition and soil development have been the most widely studied effects of arthropods on ecosystem processes (e.g., Ausmus 1977, Coleman *et al.* 2004, Crossley 1977, Eldridge 1993, 1994, Seastedt 1984, Swift 1977, Swift *et al.* 1979, Whitford 2000, Wotton *et al.* 1998). Arthropod detritivores and burrowers are relatively accessible and often can be manipulated for experimental purposes. Their key contributions to decomposition and mineralization of litter (both fine or suspended organic matter and coarse woody debris) and pedogenesis have been demonstrated in virtually all ecosystems. Indeed, some aquatic and glacial ecosystems consist of arthropod detritivores and associated microorganisms feeding entirely on allochthonous detritus (J. Edwards and Sugg 1990, Oertli 1993, J. Wallace *et al.* 1992). Effects of detritivorous and fossorial species on decomposition and soil mixing depend on the size of the organism, its food source, type and rate of detritivory, volume of displaced litter or soil, and type of saprophytic microorganisms inoculated into litter. Although most studies have addressed the effects of detritivores and burrowers on soil processes, some have documented effects of animal contributions to soil development and biogeochemical cycling to primary production as well.

I. TYPES AND PATTERNS OF DETRITIVORY AND BURROWING

A. Detritivore and Burrower Functional Groups

Functional groups of detritivorous and burrowing arthropods have been distinguished on the basis of principal food source, mode of feeding, and microhabitat preferences (e.g., J. Moore *et al.* 1988, J. Wallace *et al.* 1992). For example, functional groups can be distinguished on the basis of seasonal occurrence, habitats, and substrates (e.g., terrestrial vs. aquatic, animal vs. plant, foliage vs. wood, arboreal vs. fossorial) or particular stages in the decomposition process (N. Anderson *et al.* 1984, Hawkins and MacMahon 1989, Schowalter and Sabin 1991, Schowalter *et al.* 1998, Seastedt 1984, Siepel and de Ruiter-Dijkman 1993, Tantawi *et al.* 1996, Tullis and Goff 1987, J. Wallace *et al.* 1992, Winchester 1997, Zhong and Schowalter 1989).

General functional groupings for detritivores are based on their effect on decomposition processes. *Coarse* and *fine comminuters* are instrumental in the fragmentation of litter material. Major taxa in terrestrial ecosystems include millipedes, earthworms, termites, and beetles (coarse) and mites, collembolans, and various other small arthropods (fine). Many species are primarily *fungivores* or *bacteriovores* that fragment substrates while feeding on the surface microflora. Many fungivores and bacteriovores, including nematodes and protozoa, as well as arthropods, feed exclusively on microflora and affect the abundance and distribution of these decomposers (e.g., Santos *et al.* 1981). A number of species, including dung beetles, millipedes, and termites, are *coprophages,* either feeding on feces of larger species or reingesting their own feces following microbial decay and enrichment (Cambefort 1991, Coe 1977, Dangerfield 1994, Holter 1979, Kohlmann 1991, McBrayer 1975).

In aquatic ecosystems *scrapers* (including mayflies, caddisflies, chironomid midges, and elmid beetles), which graze or scrape microflora from mineral and organic substrates, and *shredders* (including stoneflies, caddisflies, crane flies, crayfish, and shrimp), which chew or gouge large pieces of decomposing material, represent coarse comminuters; *gatherers* (including stoneflies, mayflies, crane flies, elmid beetles, and copepods), which feed on fine particles of decomposing organic material deposited in streams, and *filterers* (mayflies, caddisflies, and black flies), which have specialized structures for sieving fine suspended organic material, represent fine comminuters (Cummins 1973, J. Wallace and Webster 1996, J. Wallace *et al.* 1992).

Xylophages are a diverse group of detritivores specialized to excavate and fragment woody litter. Major taxa include scolytid, buprestid, cerambycid and lyctid beetles, siricid wasps, carpenter ants, *Camponotus* spp., and termites (Fig. 14.1), with different species often specialized on particular wood species, sizes, or stages of decay (see Chapter 10). Most of these species either feed on fungal-colonized wood or support mutualistic, internal, or external fungi or bacteria that

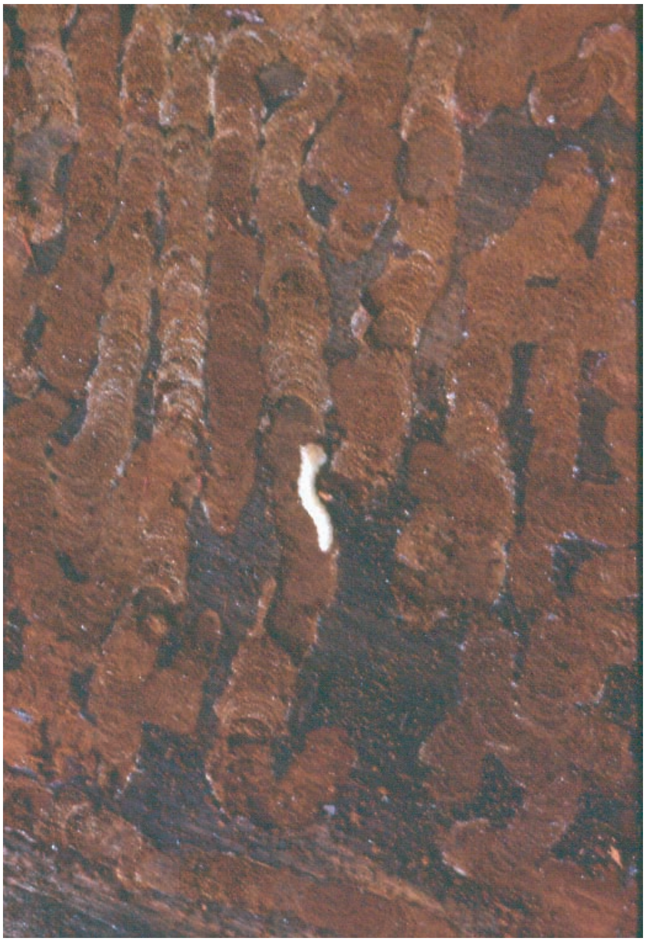


FIG. 14.1 *Melanophila* sp. (Coleoptera: Buprestidae) larva in mine in phloem of recently killed Douglas-fir tree in western Oregon. The entire phloem volume of this tree has been fragmented and converted to frass packed behind mining larvae of this species, demonstrating detritivore capacity to reduce detrital biomass. Please see extended permission list pg 572.

digest cellulose and enhance the nutritional quality of wood (e.g., Breznak and Brune 1994, Siepel and de Ruiter-Dijkman 1993; see Chapter 8).

Carrion feeders represent another specialized group that breaks down animal carcasses. Major taxa include staphylinid, sylphid, scarabaeid, and dermestid beetles; calliphorid, muscid, and sarcophagid flies; and various ants. Different species usually specialize on particular stages of decay (see Figs. 10.3 and 10.4) and on particular animal groups (e.g., reptiles vs. mammals) (E. Watson and Carlton 2003).

An important consequence of litter fragmentation by arthropods is increased surface area for microbial colonization and decomposition. Microbes also are carried, either passively through transport of microbes acquired during feeding or dispersal or actively through inoculation of mutualistic associates, to fresh surfaces during feeding.

Many detritivores redistribute large amounts of soil or detritus during foraging or feeding activities (e.g., Kohlmann 1991). However, nondetritivores also contribute to mixing of soil and organic matter. Fossorial functional groups can be distinguished on the basis of their food source and mechanism and volume of soil/detrital mixing. *Subterranean nesters* burrow primarily for shelter. Vertebrates (e.g., squirrels, woodrats, and coyotes) and many invertebrates, including crickets and solitary wasps, excavate tunnels of various sizes, usually depositing soil on the surface and introducing some organic detritus into nests. *Gatherers,* primarily social insects, actively concentrate organic substrates in colonies. Ants and termites redistribute large amounts of soil and organic matter during construction of extensive subterranean, surficial, or arboreal nests (J. Anderson 1988, Haines 1978). Subterranean species concentrate organic matter in nests excavated in soil, but many species bring fine soil particles to the surface and mix soil with organic matter in arboreal nests or foraging tunnels. These insects can affect a large volume of substrate (up to 10^3 m^3), especially as a result of restructuring and lateral movement of the colony (Hughes 1990, Moser 1963, Whitford *et al.* 1976). *Fossorial feeders,* such as gophers, moles, earthworms, mole crickets (Gryllotalpidae), and benthic invertebrates, feed on subsurface resources (plant, animal, or detrital substrates) as they burrow, constantly mixing mineral substrate and organic material in their wake.

B. Measurement of Detritivory, Burrowing, and Decomposition Rates

Evaluation of the effects of detritivory and burrowing on decomposition and soil mixing requires appropriate methods for measuring rates of these processes. Several methods have been used to measure rates of decomposition and soil mixing (Coleman *et al.* 2004).

Detritivory can be measured by providing experimental substrates and measuring colonization and consumption rates. K. Johnson and Whitford (1975) measured the rate of termite feeding on an artificial carbohydrate source and natural substrates in a desert ecosystem. Edmonds and Eglitis (1989) and Zhong and Schowalter (1989) measured the rate of wood-borer colonization and excavation in freshly cut tree boles. Dissection of wood samples is necessary for measurement of excavated volume for small insects. Radiography can be used to measure larger volumes (e.g., termite galleries).

Detritivory often has been estimated by multiplying the per capita feeding rate for each functional group by its abundance (N. Anderson *et al.* 1984, Cárcamo *et al.* 2000, Crossley *et al.* 1995, Dangerfield 1994). Cárcamo *et al.* (2000) estimated consumption of conifer needle litter by the millipede, *Harpaphe haydeniana,* at about 90 mg g^{-1} animal biomass day^{-1}, a rate that could account for processing of 36% of annual litterfall. Laboratory conditions, however, might not represent the choices of substrates available under field conditions. For example, Dangerfield (1994) noted that laboratory studies might encourage coprophagy by millipedes by restricting the variety of available substrates, thereby overrepresenting this aspect of consumption. Mankowski *et al.* (1998) used both forced-feeding and choice tests to measure wood consumption by termites when a variety of substrate types was available or restricted.

Radioisotope movement from litter provided early data on decomposition rate (Witkamp 1971). Stable isotopes (e.g., ^{13}C, ^{14}C, and ^{15}N) are becoming widely used to measure fluxes of particular organic fractions (Ågren *et al.* 1996, Andreux *et al.* 1990, Horwath *et al.* 1996, Mayer *et al.* 1995, Šantrůčková *et al.* 2000, Spain and Le Feuvre 1997, Wedin *et al.* 1995). The most widely used techniques for measuring decomposition rates in terrestrial and aquatic ecosystems involve measurement of respiration rate, comparison of litterfall and litter standing crop, and measurement of mass loss (J. Anderson and Swift 1983, Bernhard-Reversat 1982, Seastedt 1984, Witkamp 1971, Woods and Raison 1982). These techniques tend to oversimplify representation of the decomposition process and consequently yield biased estimates of decay rate.

Respiration from litter or soil represents the entire heterotrophic community as well as living roots. Most commonly, a chamber containing sodalime or a solution of NaOH is sealed over litter for a 24-hour period, and CO_2 efflux is measured as the weight gain of sodalime or volume of acid neutralized by NaOH (N. Edwards 1982). Comparison of respiration rates between plots with litter present and plots with litter removed provides a more accurate estimate of respiration rates from decomposing litter, but separation of litter from soil is difficult and often arbitrary (J. Anderson and Swift 1983, Woods and Raison 1982). More recently, gas chromatography and infrared gas analysis (IRGA) have been used to measure CO_2 efflux (Nakadai *et al.* 1993, Parkinson 1981, Raich *et al.* 1990).

The ratio of litterfall mass to litter standing crop provides an estimate of the decay constant, k, when litter standing crop is constant (Olson 1963). Decay rate can be calculated if the rate of change in litter standing crop is known (Woods and Raison 1982). This technique also is limited by the difficulty of separating litter from underlying soil for mass measurement (J. Anderson and Swift 1983, Spain and Le Feuvre 1987, Woods and Raison 1982).

Weight loss of fine litter has been measured using tethered litter, litterbags, and litterboxes. Tethering allows litter to take a natural position in the litterbed and does not restrict detritivore activity or alter microclimate but is subject to loss of fragmented material and difficulty in separating litter in late stages of decay from surrounding litter and soil (N. Anderson *et al.* 1984, Birk 1979, Witkamp and Olson 1963, Woods and Raison 1982).

Litterbags provide a convenient means for studying litter decomposition (Crossley and Hoglund 1962, C. Edwards and Heath 1963). Litterbags retain selected litter material, and mesh size can be used to selectively restrict entry by larger functional groups (e.g., C. Edwards and Heath 1963, Wise and Schaefer 1994). However, litterbags may alter litter microclimate and restrict detritivore activity, depending on litter conformation and mesh size. Moisture retention between flattened leaves apparently is independent of mesh size. Exclusion of larger detritivores by small mesh sizes has little effect, at least until litter has been preconditioned by microbial colonization (J. Anderson and Swift 1983, Macauley 1975, O'Connell and Managé 1983, Spain and Le Feuvre 1987, Woods and Raison 1982). However, exclusion of predators by small mesh sizes can significantly affect detritivore abundances and decomposition processes (M. Hunter *et al.* 2003). Large woody litter (e.g., tree boles) also can be enclosed in mesh cages for experimental restriction of colonization by wood-boring insects. The potential interference with decomposition by small mesh sizes has been addressed in some studies by minimizing leaf overlap (and prolonged moisture retention) in larger litterbags, using small mesh on the bottom to retain litter fragments and large mesh on the top to maximize exchange of moisture and detritivores, and measuring decomposition over several years to account for differences resulting from changing environmental conditions (J. Anderson *et al.* 1983, Cromack and Monk 1975, Woods and Raison 1982, 1983). Despite limitations, litterbags have been the simplest and most widely used method for measuring decomposition rates and probably provide reasonably accurate estimates (Seastedt 1984, Spain and Le Feuvre 1987, Woods and Raison 1982).

More recently, litterboxes have been designed to solve problems associated with litterbags. Litterboxes can be inserted into the litter, with the open top providing unrestricted exchange of moisture and detritivores (Seastedt and Crossley 1983), or used as laboratory microcosms to study effects of decomposers (Haimi and Huhta 1990, Huhta *et al.* 1991). Similar constructions can be incorporated into streams for assessment of detrital decomposition (March *et al.* 2001).

Measurement of wood decomposition presents special problems, including the long timeframe of wood decomposition; the logistical difficulties of experimental placement; and manipulation of large, heavy material. Decomposition of large woody debris represents one of the longest ecological processes, often spanning centuries (Harmon *et al.* 1986). This process traditionally was studied by comparing mass of wood of estimated age to the mass expected for the estimated original volume, based on particular tree species. However, decomposition of some wood components begins only after lag times of up to several years, decomposition of standing tree boles is much slower than fallen boles, and differences in chemistry and volume between bark and wood components affect overall decay rates (Harmon *et al.* 1986, Schowalter *et al.* 1998).

Abundances of detritivore functional groups can be manipulated to some extent by use of microcosms (Setälä and Huhta 1991, Setälä *et al.* 1996), selective biocides or other exclusion techniques (Crossley and Witkamp 1964,

C. Edwards and Heath 1963, González and Seastedt 2001, E. Ingham *et al.* 1986, Macauley 1975, Pringle *et al.* 1999, Santos and Whitford 1981, Schowalter *et al.* 1992, Seastedt and Crossley 1983, J. Wallace *et al.* 1991) or by adding or simulating detritivores in new substrates (González and Seastedt 2001, Progar *et al.* 2000). Naphthalene and chlordane in terrestrial studies (Crossley and Witkamp 1964, Santos and Whitford 1981, Seastedt and Crossley 1983, Whitford 1986) and methoxychlor or electric fields in aquatic studies (Pringle *et al.* 1999, J. Wallace *et al.* 1991) have been used to exclude arthropods. However, E. Ingham (1985) reviewed the use of selective biocides and concluded that none had effects limited to a particular target group, limiting their utility for evaluating effects of individual functional groups. Furthermore, Seastedt (1984) noted that biocides provide a carbon and, in some cases, nitrogen source that may alter the activity or composition of microflora. Mesh sizes of litterbags (see later in this chapter) can be manipulated to exclude detritivores larger than particular sizes, but this technique often alters litter environment and may reduce fragmentation, regardless of faunal presence (Seastedt 1984).

Few experimental studies have compared effects of manipulated abundances of boring insects on wood decomposition (Edmonds and Eglitis 1989, Progar *et al.* 2000, Schowalter *et al.* 1992). Some studies have compared species or functional group abundances in wood of estimated age or decay class, but such comparison ignores the effect of initial conditions on subsequent community development and decomposition rate. Prevailing weather conditions, the physical and chemical condition of the wood at the time of plant death, and prior colonization determine the species pools and establishment of potential colonists. Penetration of the bark and transmission by wood-boring insects generally facilitate microbial colonization of subcortical tissues (Ausmus 1977, Dowding 1984, Swift 1977). Käärik (1974) reported that wood previously colonized by mold fungi (Ascomyctina and Fungi Imperfecti) was less suitable for establishment by decay fungi (Basidiomycotina) than was uncolonized wood. Mankowski *et al.* (1998) reported that wood consumption by termites was affected by wood species and fungal preconditioning. Hence, experiments should be designed to evaluate effects of species or functional groups on decomposition over long time periods using wood of standard size, composition, and condition.

Assessing rates of burrowing and mixing of soil and litter is even more problematic. A few studies have provided limited data on the volume of soil affected through excavation of ant nests (Moser 1963, Tschinkel 1999, Whitford *et al.* 1976). However, the difficulty of separating litter from soil limits measurement of mixing. Tunneling through woody litter presents similar problems. Zhong and Schowalter (1989) dissected decomposing tree boles to assess volume of wood excavated or mixed among bark, wood, and fecal substrates.

C. Spatial and Temporal Patterns in Processing of Detritus and Soil

All, or most, dead organic matter eventually is catabolized to CO_2, water, and energy, reversing the process by which energy and matter were fixed in primary production. Some materials are decomposed more readily than are others; some processes release carbon primarily as methane; and some enter long-term storage as humus, peat, coal, or oil. Moisture, litter quality (especially lignin and nitrogen content), and oxygen supply are extremely important to the decomposition process (Aerts 1997, Birk 1979, Cotrufo *et al.* 1998, Fogel and Cromack 1977, Fonte and Schowalter 2004, González and Seastedt 2001, Meentemeyer 1978, Progar *et al.* 2000, Seastedt 1984, Tian *et al.* 1995, Whitford *et al.* 1981). For example, animal carrion is readily digestible by many organisms and decomposes rapidly (Payne 1965), whereas some plant materials, especially those composed largely of lignin and cellulose, can be decomposed only by relatively few species of fungi, bacteria, or protozoa and may require long time periods for complete decomposition (Harmon *et al.* 1986). Conifer litter tends to decompose more slowly than does angiosperm litter because of low nitrogen content and high lignin content. Low soil or litter pH inhibits decomposition. Rapid burial or saturation with water inhibits decomposition of litter because of limited oxygen availability. Submerged litter is degraded primarily by aquatic gougers and scrapers that slowly fragment and digest consumed organic matter from the surface inward (N. Anderson *et al.* 1984).

Decomposition processes differ among ecosystem types. Physical factors may predominate in xeric ecosystems where decomposition of exposed litter reflects catabolic effects of ultraviolet light. Decomposition resulting from biological processes is favored by warm, moist conditions. Decomposition is most rapid in wet tropical ecosystems, where litter disappears quickly, and slowest in desert, tundra, and boreal ecosystems because of dry or cold conditions. González and Seastedt (2001) and Heneghan *et al.* (1999) compared decomposition of a common litter species between tropical and temperate ecosystems and demonstrated that decomposition was consistently higher in the tropical wet forests. Nevertheless, decomposition may continue underground, or under snow in tundra and boreal regions, if temperature and moisture are adequate (e.g., Santos *et al.* 1981). As noted earlier in this section, decomposition rates may be lower in aquatic ecosystems as a result of saturation and limited oxygen supply. Low decomposition rates generally result in the accumulation of large standing crops of woody and fine litter.

Different groups of detritivores and decomposers dominate different ecosystems. For example, shredders and gatherers were more abundant in pools and headwater streams, characterized by substantial inputs of largely unfragmented organic matter, whereas filter-feeders were more abundant in high gradient sections or higher-order streams (the Little Tennessee River), characterized by highly fragmented, suspended organic matter (Fig. 14.2). Fungi and associated fungivores (e.g., oribatid mites and Collembola) are more prevalent in forests, whereas bacteria, bacteriovores, especially prostigmatid mites and Collembola, and earthworms are more prevalent in grasslands (Seastedt 2000). Termites are the most important detritivores in arid and semi-arid ecosystems and may largely control decomposition processes in forest and grassland ecosystems (K. E. Lee and Butler 1977, Whitford 1986). J. Jones (1989, 1990) reported that termites in dry tropical ecosystems in Africa so thoroughly decompose organic matter that

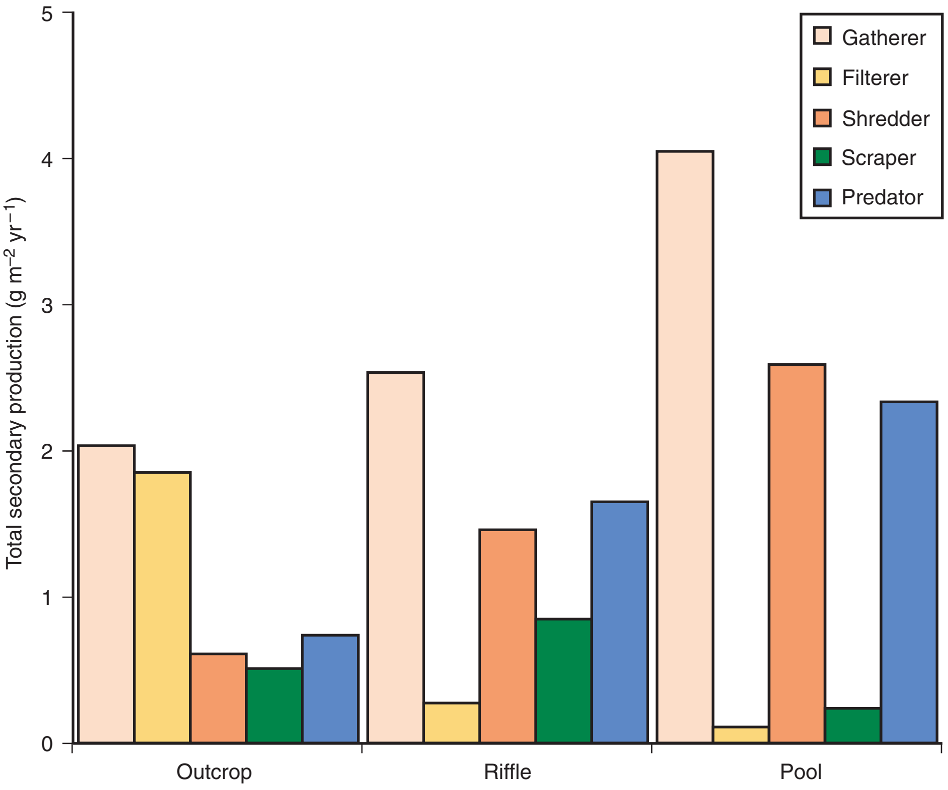


FIG. 14.2 Annual secondary production for aquatic functional groups in bedrock outcrop, riffle, and pool habitats of upper Ball Creek, North Carolina, during July 1983–June 1984. Data from Huryn and Wallace (1987). Please see extended permission list pg 572.

little or no carbon is incorporated into the soil. Wood-boring insects occur only in ecosystems with woody litter accumulation and are vulnerable to loss of this resource in managed forests (Grove 2002). Dung feeders are important in ecosystems where vertebrate herbivores are abundant (Coe 1977, Holter 1979).

The relative contributions of physical and biological factors to pedogenesis vary among ecosystems. Erosion and earth movements (e.g., soil creep and landslides) mix soil and litter in ecosystems with steep topography or high wind or raindrop impact on surface material. Burrowing animals are common in ecosystems with loose substrates suitable for excavation. Grasslands and forests on sandy or loamy soils support the highest diversity and abundances of burrowers. Ants often excavate nests through rocky, or other, substrates, which would preclude burrowing by larger or softer-bodied animals and are the dominant burrowers in many ecosystems.

Distinct temporal patterns in decomposition rates often reflect either the preconditioning requirements for further degradation or the inhibition or facilitation of new colonizers by established groups. For example, leaching of toxic chemicals may be necessary before many groups are able to colonize litter (Barz and Weltring 1985). M. Hulme and Shields (1970) and Käärik (1974) reported that wood decay is inhibited by competition for labile carbohydrates, necessary for early growth of decay fungi, by nondecay fungi. However, Blanchette and Shaw (1978) found that decay fungus growth in wood with bacteria and yeasts was twice that in wood without bacteria and yeasts, presumably because bacteria and yeasts provide fixed nitrogen, vitamins, and other nutrients while exploiting carbohydrates from lignocellulose degradation. Microbes usually require bark penetration, and often inoculation, by insects to colonize woody litter. Many saprophagic arthropods require some preconditioning of litter by bacteria, fungi, or other arthropods prior to feeding. Small comminuters usually feed on fragments or feces left by larger comminuters (O'Connell and Menagé 1983). Shredders in streams convert coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) that can be acquired by filterers (J. Wallace and Webster 1996, J. Wallace *et al.* 1991). Santos and Whitford (1981) reported that a consistent succession of microarthropods was related to the percentage of organic matter lost.

Decomposition often begins long before detritus reaches the soil. Considerable detrital accumulation occurs in forest canopies (Coxson and Nadkarni 1995, Paoletti *et al.* 1991). Processes of decomposition and pedogenesis in these suspended sediments are poorly known, but Paoletti *et al.* (1991) reported that suspended soils associated with bromeliads in a Venezuelan cloud forest had higher concentrations of organic matter, nitrogen, calcium, and magnesium and higher densities (based on bulk density of soil) of macroinvertebrates and microinvertebrates than did forest floor soils. However, rates of litter decomposition as measured in litterbags were similar in the canopy and forest floor. Oribatid mites and Collembola are the most abundant detritivores in temperate and tropical forest canopies (Paoletti *et al.* 1991, Schowalter and Ganio 1998, Walter and O'Dowd 1995, Winchester 1997), and many are canopy specialists that do not occur on the forest floor (Winchester *et al.* 1999).

Decomposition is an easily modeled process. Usually, an initial period of leaching or microbial oxidation of simple organic molecules results in a short-term, rapid loss of mass, followed by a longer-term, slower decay of recalcitrant compounds. Decomposition of foliage litter has been expressed as a single- or double-component negative exponential model (Olson 1963):

$$N_t = S_0 e^{-kt} + L_0 e^{-kt} \tag{14.1}$$

where N_t is mass at time t, S_0 and L_0 are masses in short- and long-term components, and respectively; and k's are the respective decay constants. The short-term rate of decay reflects the mass of labile organic molecules, and the long-term rate of decay reflects lignin content and actual evapotranspiration (AET) rate, based on temperature and moisture conditions (Meentemeyer 1978, Seastedt 1984). Long-term decay constants for foliage litter range from -0.14 year^{-1} to -1.4 year^{-1}, depending on nutritional value for decomposers (Table 14.1) (Laskowski *et al.* 1995, Seastedt 1984, Schowalter *et al.* 1991). Decay constants for wood range from -0.004 year^{-1} to -0.5 year^{-1} (Harmon *et al.* 1986). Schowalter *et al.* (1998) monitored decomposition of freshly cut oak, *Quercus* spp., logs over a 5-year period and found that a 3-component exponential model was necessary to

TABLE 14.1 Annual decay rates of various litter types with microarthropods present and experimentally excluded.

Litter type	Decay constant (yr^{-1})			Faunal effect (%)	Reference
	Without fauna	With fauna	Faunal component		
Dogwood foliage[a] (*Cornus florida*)	–0.69	–0.82	–0.13	16	Cromack (unpubl), Seastedt and Crossley (1980, 1983)
Chestnut oak foliage[a] (*Quercus prinus*)	–0.48	–0.50	–0.02	4	Cromack (unpubl), Seastedt and Crossley (1980, 1983)
White oak foliage (*Quercus alba*)	–0.60	–0.92	–0.32	35	Witkamp and Crossley (1966)
Beech foliage[a] (*Fagus sylvatica*)	–0.41	–0.50	–0.09	18	J. Anderson (1973)
Chestnut foliage[a] (*Castanea sativa*)	–0.27	–0.28	–0.01	4	J. Anderson (1973)
Mixed hardwood foliage	–0.40	–0.70	–0.30	43	Cromack (1973)
Eucalypt foliage[b] (*Eucalyptus pauciflora*)	–0.45	–0.73	–0.28	38	Madge (1969)
Eucalypt foliage[c] (*Eucalyptus pauciflora*)	–0.69	–0.73	–0.04	8	Madge (1969)
Shinnery oak foliage (*Quercus harvardii*)	–0.22	–0.43	–0.21	49	Elkins and Whitford (1982)
Broomsedge (*Andropogon virginicus*)	–0.30	–0.36	–0.06	17	J. Williams and Wiegert (1971)
Blue grama grass (*Bouteloua gracilis*)	–0.14	–0.45	–0.31	69	Vossbrinck et al. (1979)
Mixed pasture grasses					
Surface	–1.15	–1.24	–0.09	7	Curry (1969)
Buried	–1.55	–1.34	+0.21	–16	Curry (1969)
Mixed tundra grasses[a]	–0.22	–0.32	–0.10	31	Douce and Crossley (1982)

[a] Mean values for experiments replicated over sites (Anderson 1973, Douce and Crossley 1982) or years (Cromack unpubl., Seastedt and Crossley 1980, 1983).

[b] Control versus insecticide comparison.

[c] Medium mesh (1 mm) versus fine mesh (0.5 mm) comparison. Fine mesh bags probably did not exclude all microarthropods.

From Seastedt (1984) with permission from the *Annual Review of Entomology,* Vol. 29, © 1984 by Annual Reviews.

account for differential decay rates among bark and wood tissues. An initial decay rate of –0.12 year^{-1} during the first year reflected primarily the rapid loss of the nutritious inner bark (phloem), which largely disappeared by the end of the second year as a result of rapid exploitation by insects and fungi. An intermediate decay rate of –0.06 year^{-1} for years 2–5 reflected the slower decay rate for sapwood and outer bark, and a long-term decay rate of –0.012 year^{-1} was predicted, based on the slow decomposition of heartwood.

Decomposition often is not constant but shows seasonal peaks and annual variation that reflect periods of suitable temperature and moisture for decomposers. Patterns of nutrient mineralization from litter reflect periods of storage and loss, depending on activities of various functional groups. For example, Schowalter and Sabin (1991) reported that nitrogen and calcium content of decomposing Douglas-fir, *Pseudotsuga menziesii,* needle litter, in litterbags, in western Oregon peaked in spring each year, when microarthropod abundances were lowest, and declined during winter, when microarthropod abundances were highest. High rates of comminution by microarthropods and decay by microorganisms during the wet winters likely contributed to release of nutrients from litter, whereas reduced comminution and decay during dry springs and summers led to nutrient immobilization in microbial biomass. Similarly, fluctuating concentrations of nutrients in decomposing oak wood over time probably reflect patterns of colonization and mobilization (Schowalter *et al.* 1998).

II. EFFECTS OF DETRITIVORY AND BURROWING

Arthropod detritivores and burrowers directly and indirectly affect decomposition, carbon flux, biogeochemical cycling, pedogenesis, and primary production. The best-known effects are on decomposition and mineralization (Seastedt 1984, Coleman *et al.* 2004). Detritivorous and fossorial arthropods are capable of significantly affecting global carbon budgets and ecosystem capacity to store and release nutrients and pollutants.

A. Decomposition and Mineralization

An extensive literature has addressed the effects of detritivores on decomposition and mineralization rates (Coleman *et al.* 2004). Generally, the effect of arthropods on the decay rate of litter can be calculated by subtracting the decay rate when arthropods are excluded from the decay rate when arthropods are present (see Table 14.1). Detritivores affect decomposition and mineralization processes, including fluxes of carbon as CO_2 or CH_4, by fragmenting litter and by affecting rates of microbial catabolism of organic molecules. The magnitude of these effects depends on the degree to which feeding increases the surface area of litter and inoculates or reduces microbial biomass.

1. Comminution

Large comminuters are responsible for the fragmentation of large detrital materials into finer particles that can be processed by fine comminuters and saprophytic microorganisms. Cuffney *et al.* (1990) and J. Wallace *et al.* (1991) reported that 70% reduction in abundance of shredders from a small headwater stream in North Carolina, United States, reduced leaf litter decay rates by 25–28% and export of fine particulate organic matter by 56%. As a result, unprocessed leaf litter accumulated (J. Wallace *et al.* 1995). Wise and Schaefer (1994) found that excluding macroarthropods and earthworms from leaf litter of selected plant species in a beech forest reduced decay rates 36–50% for all litter types except fresh beech litter. When all detritivores were excluded, comparable reduction in decay rate was 36–93%, indicating the prominent role of large comminuters in decomposition. Tian *et al.* (1995) manipulated abundances of millipedes and earthworms in tropical agricultural ecosystems. They found that millipedes alone significantly accounted for 10–65% of total decay over a 10-week period. Earthworms did not affect decay significantly by themselves, but earthworms and millipedes combined significantly accounted for 11–72% of total decay. Haimi and Huhta (1990) demonstrated that earthworms significantly increased mass loss of litter by 13–41%. N. Anderson *et al.* (1984) noted that aquatic xylophagous tipulid larvae fragmented >90% of decayed red alder, *Alnus rubra,* wood in a 1-year period.

Termites have received considerable attention because of their substantial ecological and economic importance in forest, grassland, and desert ecosystems. Based on laboratory feeding rates, K. E. Lee and Butler (1977) estimated wood consumption by termites in dry sclerophyll forest in South Australia. They reported that wood consumption by termites was equivalent to about 25% of annual woody litter increment and 5% of total annual litterfall. Based on termite exclusion plots, Whitford *et al.* (1982) reported that termites consumed up to 40% of surficial leaf litter in a warm desert ecosystem in the southwestern United States (Fig. 14.3). Overall, termites in this ecosystem consumed at least 50% of estimated annual litterfall (K. Johnson and Whitford 1975, Silva *et al.* 1985). N. M. Collins (1981) reported that termites in tropical savannas in West Africa consumed 60% of annual wood fall and 3% of annual leaf fall (24% of total litter production), but fire removed 0.2% of annual wood fall and 49% of annual leaf fall (31% of total litter production). In that study, fungus-feeding Macrotermitinae were responsible for 95% of the litter removed by termites. Termites apparently consume virtually all litter in tropical savannas in East Africa (J. Jones 1989, 1990). Termites consume a lower proportion of annual litter inputs in more mesic ecosystems. N. M. Collins (1983) reported that termites consumed about 16% of annual litter production in a Malaysian rainforest receiving 2000 mm precipitation year^{-1} and 1–3% of annual litter production in a Malaysian rainforest receiving 5000 mm precipitation year^{-1}.

Accumulation of dung from domestic mammalian grazers has become a serious problem in many arid and semi-arid ecosystems. Termites removed as much as 100% of cattle dung over 3 months in Kenya (Coe 1977), 80–85% over 5–9 months in tropical pastures in Costa Rica (Herrick and Lal 1996), and 47% over 4 months in the Chihuahuan Desert in the southwestern United States (Whitford *et al.* 1982). In the absence of termites, dung would require 25–30 years to disappear (Whitford 1986). Dung beetles (Scarabaeidae) and earthworms also

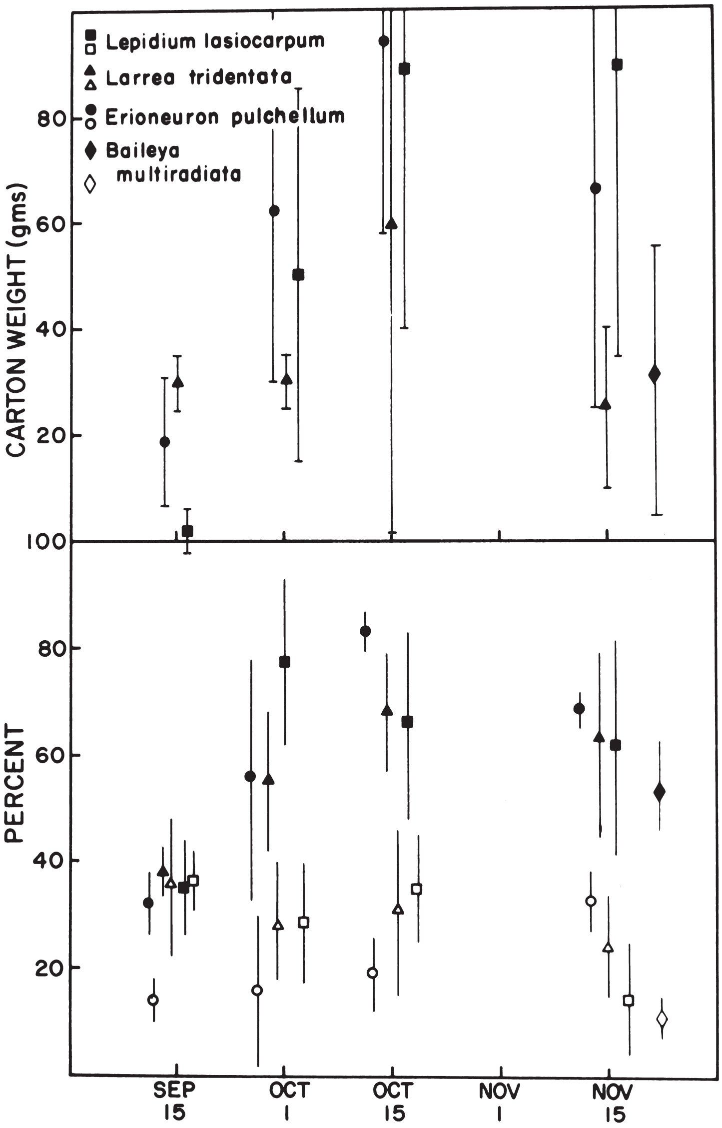


FIG. 14.3 Rate of gallery carton deposition (*top*) and mass loss (*bottom*) of creosote bush, *Larrea tridentata,* and fluff grass, *Erioneuron pulchellum,* foliage when subterranean termites were present (*black symbols*) or absent (*white symbols*) in experimental plots in southern New Mexico. Litter (10 g) was placed in aluminum mesh cylinders on the soil surface on August, 15, 1979. Vertical lines represent standard errors. From Whitford *et al.* (1982) with permission from Springer-Verlag. Please see extended permission list pg 573.

are important consumers of dung in many tropical and subtropical ecosystems (e.g., Coe 1977, Holter 1979, Kohlmann 1991).

Relatively few studies have provided estimates of wood consumption by bark- and wood-boring insects, despite their recognized importance to wood decomposition. Zhong and Schowalter (1989) reported that bark beetles consumed 0.1–7.6% of inner bark and wood-boring beetles consumed an additional

0.05–2.3% during the first year of decomposition, depending on conifer tree species. Ambrosia beetles consumed 0–0.2% of the sapwood during the first year. Schowalter *et al.* (1998) found that virtually the entire inner bark of oak logs was consumed by beetles during the first 2 years of decomposition, facilitating separation of the outer bark and exposing the sapwood surface to generalized saprophytic microorganisms. Edmonds and Eglitis (1989) used exclusion techniques to demonstrate that, over a 10-year period, bark beetles and wood-borers increased decay rates of large Douglas-fir logs (42 cm diameter at breast height) by 12% and of small logs (26 cm diameter at breast height) by 70%.

Payne (1965) explored the effects of carrion feeders on carrion decay during the summer in South Carolina, United States. He placed baby pig carcasses under replicated treatment cages, open at the bottom, that either permitted or restricted access to insects. Carcasses were weighed at intervals. Carcasses exposed to insects lost 90% of their mass in 6 days, whereas carcasses protected from insects lost only 30% of their mass in this period, followed by a gradual loss of mass, with 20% mass remaining in mummified pigs after 100 days.

Not all studies indicate significant effects of litter fragmentation by macroarthropods. Setälä *et al.* (1996) reported that manipulation of microarthropods, mesoarthropods, and macroarthropods in litter baskets resulted in slower decay rates in the presence of macroarthropods. Most litter in baskets with macroarthropods (millipedes and earthworms) was converted into large fecal pellets that decayed slowly.

A number of studies have demonstrated that microarthropods are responsible for up to 80% of the total decay rate, depending on litter quality and ecosystem (see Table 14.1, Fig. 14.4) (Coleman *et al.* 2004, González and Seastedt 2001, Heneghan *et al.* 1999, Seastedt 1984). Seastedt (1984) suggested that an apparent, but insignificant, inverse relationship between decay rate as a result of microarthropods and total decay rate indicated a greater contribution of arthropods to decomposition of recalcitrant litter fractions compared to more labile fractions. Tian *et al.* (1995) subsequently reported that millipedes and earthworms contributed more to the decomposition of plant residues with high C : N, lignin, and polyphenol contents than to high-quality plant residues.

2. Microbial Respiration

Microbial decomposers are responsible for about 95% of total heterotrophic respiration in soil. Arthropods generally increase microbial respiration rates and carbon flux but may reduce respiration rates if they overgraze microbial resources (Huhta *et al.* 1991, Seastedt 1984). Several studies have documented increased microbial respiration as a result of increased arthropod access to detrital substrate and stimulation of microbial production.

Litter fragmentation greatly increases the surface area exposed for microbial colonization. Zhong and Schowalter (1989) reported that ambrosia beetle densities averaged 300 m^{-2} bark surface in Douglas-fir and western hemlock, *Tsuga heterophylla,* logs, and their galleries extended 9–14 cm in 4–9 cm thick sapwood, indicating that considerable sapwood volume was made accessible to microbes colonizing gallery walls. The entire sapwood volume of these logs was colonized

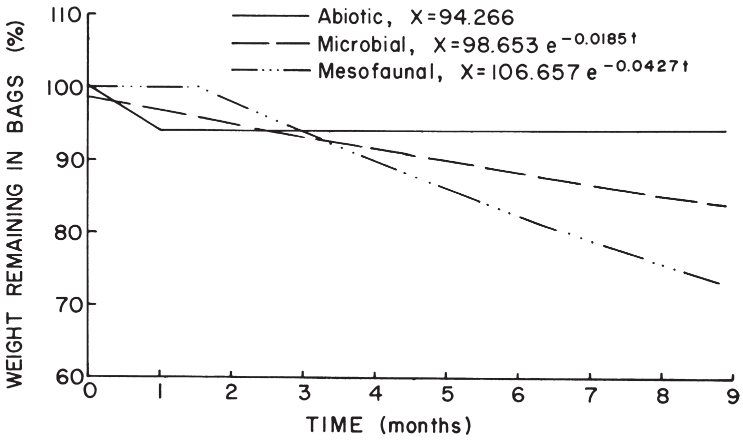


FIG. 14.4 Decomposition rate of blue grama grass in litterbags treated to permit decomposition by abiotic factors alone, abiotic factors + microbes, and abiotic factors + microbes + mesofauna (microarthropods). Decomposition in the abiotic treatment was insignificant after the first month; decomposition showed a 2-month time lag in the treatment including mesofauna. From Vossbrinck *et al.* (1979) with permission from the Ecological Society of America.

by various fungi within the first year after logs were cut (Schowalter *et al.* 1992). Mixing of organic material and microbes during passage through detritivore guts ensures infusion of consumed litter with decomposers and may alter litter quality in ways that stimulate microbial production (Maraun and Scheu 1996). Gut mixing is especially important for species such as termites and other wood-borers that require microbial digestion of cellulose and lignin into labile carbohydrates (Breznak and Brune 1994).

Many arthropods directly transport and inoculate saprophytic microorganisms into organic residues. For example, Schowalter *et al.* (1992) documented transport of a large number of fungal genera by wood-boring insects. Some of these fungi are mutualists that colonize wood in advance of insects and degrade cellulose into labile carbohydrates that subsequently are used by insects (Bridges and Perry 1985, French and Roeper 1972, Morgan 1968). Others may be acquired accidentally by insects during feeding or movement through colonized material (Schowalter *et al.* 1992). Behan and Hill (1978) documented transmission of fungal spores by oribatid mites.

Fungivorous and bacteriophagous arthropods stimulate microbial activity by maximizing microbial production. As discussed for herbivore effects on plants in Chapter 12, low to moderate levels of grazing often stimulate productivity of the microflora by alleviating competition, altering microbial species composition, and gouging new detrital surfaces for microbial colonization. Microarthropods also can stimulate microbial respiration by preying on bacteriophagous and mycophagous nematodes (Seastedt 1984, Setälä *et al.* 1996). Higher levels of grazing may depress microbial biomass and reduce respiration rates (Huhta *et al.* 1991, Seastedt 1984).

Seastedt (1984) suggested a way to evaluate the importance of three pathways of microbial enhancement by arthropods, based on the tendency of microbes to immobilize nitrogen in detritus until C : N ratio approaches 10–20 : 1. Where arthropods affect decomposition primarily through comminution, nitrogen content of litter should be similar with or without fauna. Alternatively, where arthropods stimulate microbial growth and respiration rates, the C : N ratio of litter with fauna should be less than the ratio without fauna. Finally, where arthropods graze microbial tissues as fast as they are produced, C : N ratio of litter should be constant, and mass should decrease.

Seasonal variation in arthropod effects on microbial production and biomass may explain variable results and conclusions from earlier studies. Maraun and Scheu (1996) reported that fragmentation and digestion of beech leaf litter by the millipede, *Glomeris marginata,* increased microbial biomass and respiration in February and May but reduced microbial biomass and respiration in August and November. They concluded that millipede feeding generally increased nutrient (nitrogen and phosphorus) availability but that these nutrients were only used for microbial growth when carbon resources were adequate, as occurred early in the year. Depletion of carbon resources relative to nutrient availability in detritus limited microbial growth later in the year.

Although CO_2 is the major product of litter decomposition, incomplete oxidation of organic compounds occurs in some ecosystems, resulting in evolution of other trace gases, especially methane (Khalil *et al.* 1990). P. Zimmerman *et al.* (1982) first suggested that termites could contribute up to 35% of global emissions of methane. A number of arthropod species, including most tropical representatives of millipedes, cockroaches, termites, and scarab beetles, are important hosts for methanogenic bacteria and are relatively important sources of biogenic global methane emissions (Hackstein and Stumm 1994).

Termites have received the greatest attention as sources of methane because their relatively sealed colonies are warm and humid, with low oxygen concentrations that favor fermentation processes and emission of methane or acetate (Brauman *et al.* 1992, Wheeler *et al.* 1996). Thirty of 36 temperate and tropical termite species assayed by Brauman *et al.* (1992), Hackstein and Stumm (1994), and Wheeler *et al.* (1996) produced methane, acetate, or both. Generally, acetogenic bacteria outproduce methanogenic bacteria in wood- and grass-feeding termites, but methanogenic bacteria are much more important in fungus-growing and soil-feeding termites (Brauman *et al.* 1992).

P. Zimmerman *et al.* (1982) suggested that tropical deforestation and conversion to pasture and agricultural land could increase the biomass and methane emissions of fungus-growing and soil-feeding termites, but Martius *et al.* (1996) concluded that methane emissions from termites in deforested areas in Amazonia would not contribute significantly to global methane fluxes. Khalil *et al.* (1990), Martius *et al.* (1993), and Sanderson (1996) calculated CO_2 and methane fluxes based on global distribution of termite biomass and concluded that termites contribute ca 2% of the total global flux of CO_2 (3500 tg year^{-1}) and 4–5% of the global flux of methane (≤20 tg year^{-1}) (Fig. 14.5). However, emissions of CO_2 by termites are 25–50% of annual emissions from fossil fuel com-

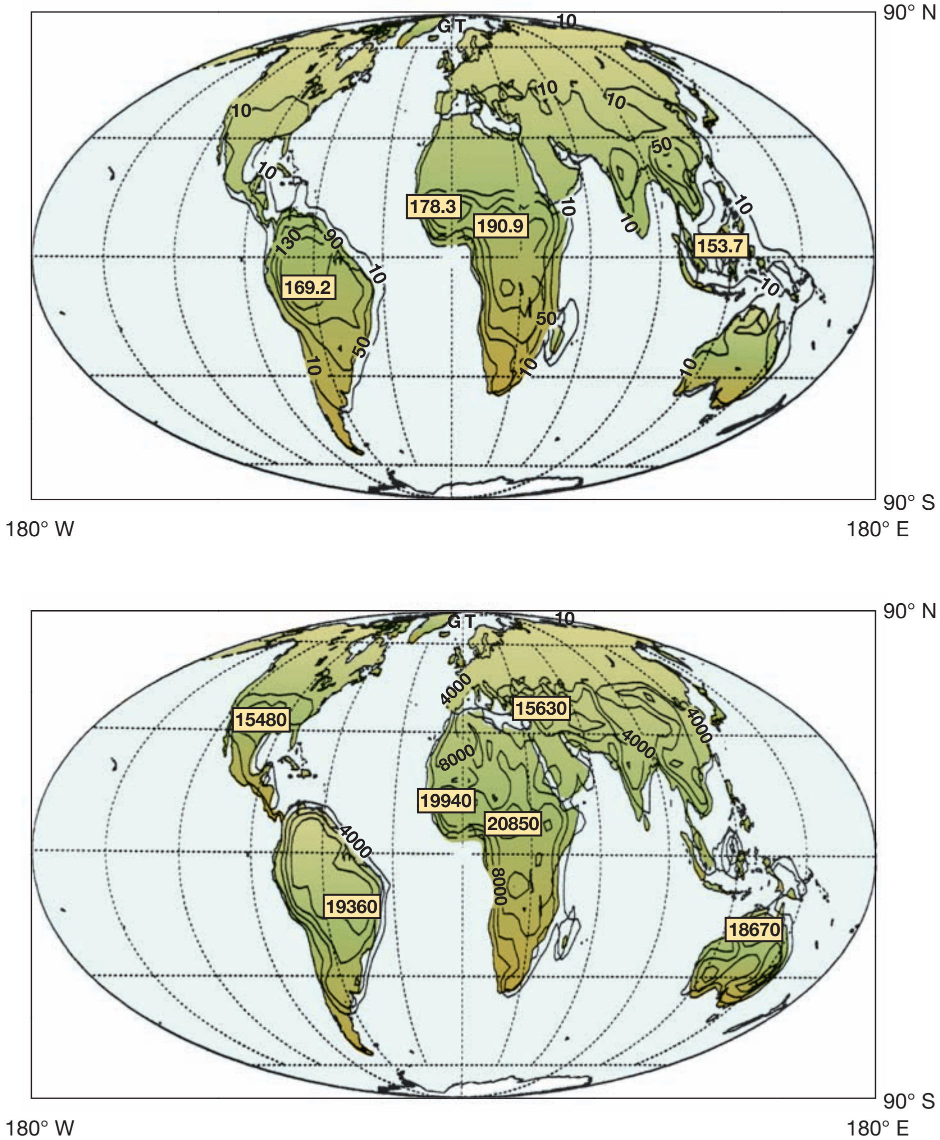


FIG. 14.5 Geographic distribution of emissions of methane (*top)* and carbon dioxide (*bottom)* by termites. Units are 10^6 kg yr^{-1}. From Sanderson (1996) courtesy of the American Geophysical Union.

bustion (Khalil *et al.* 1990). Contributions to atmospheric composition by this ancient insect group may have been more substantial prior to anthropogenic production of CO_2, methane, and other trace gases.

3. Mineralization

Measurements of changes in elemental concentrations represent net mineralization rates. Net mineralization includes loss of elements as a result of mineralization and accumulation by microflora of elements entering as microparticulates, precipitation, and leachate or transferred (e.g., via hyphae) from other organic material (Schowalter *et al.* 1998, Seastedt 1984). Although microbial biomass usually is a negligible component of litter mass, microbes often represent a large proportion of the total nutrient content of decomposing detritus and significantly affect the nutrient content of the litter–microbial complex (e.g., Seastedt 1984). Arthropods affect net mineralization in two measurable ways: through mass loss and assimilation of consumed nutrients and through effects on nutrient content of the litter–microbe system. Seastedt (1984) proposed the following equation to indicate the relative effect of arthropods on mineralization:

$$\mathrm{Y} = [\%\ \mathrm{mass_i} / \%\ \mathrm{mass_x}) \times (\mathrm{concentration_i} / \mathrm{concentration_x}) \qquad (14.2)$$

where Y is the relative arthropod effect, % $\mathrm{mass_i}$ is the percentage of initial mass remaining that has been accessible to arthropods, % $\mathrm{mass_x}$ is the percentage of initial mass remaining that has been unavailable to arthropods, and $\mathrm{concentration_i}$ and $\mathrm{concentration_x}$ are the respective concentrations of a given element. Net immobilization of an element is indicated by $\mathrm{Y} > 1$, and net loss is indicated by $\mathrm{Y} < 1$. Temporal changes in nutrient content depend on the structural position of the element within organic molecules, microbial use of the element, and the form and amounts of the element entering the detritus from other sources.

Nitrogen generally is considered to be the element most likely to limit growth of plants and animals, and its release from decomposing litter often is correlated with plant productivity (Vitousek 1982). As noted earlier in this chapter, saprophytic microbes usually immobilize nitrogen until sufficient carbon has been respired to make carbon or some other element more limiting than nitrogen (Maraun and Scheu 1996, Schowalter *et al.* 1998, Seastedt 1984). Thereafter, the amount of nitrogen released should equal the amount of carbon oxidized. Microbes have considerable capacity to absorb nitrogen from precipitation, canopy leachate, and animal excrement (see Fig. 12.14) (Lovett and Ruesink 1995, Seastedt and Crossley 1983, Stadler and Müller 1996), permitting nitrogen mineralization and immobilization even at high C : N ratios. Generally, exclusion of microarthropods decreases the concentration of nitrogen in litter, but the absolute amounts of nitrogen in litter are decreased or unaffected by microarthropod feeding activities (Seastedt 1984).

Yokoyama *et al.* (1991) compared nitrogen transformations among cattle dung (balls) colonized by dung beetles, *Onthophagus lenzii*; uncolonized dung; and residual dung remaining after beetle departure. They reported that dung beetles reduced ammonia volatilization from dung 50% by reducing pH and ammonium concentration in dung (through mixing of dung and soil). However, dung beetles increased denitrification 2–3-fold by increasing the rate of nitrate formation. Dung beetles also increased nitrogen fixation 2–10-fold, perhaps by reducing inorganic nitrogen concentrations in a substrate of easily decomposable organic matter.

Phosphorus concentrations often show initial decline as a result of leaching but subsequently reach an asymptote determined by microbial biomass (Schowalter and Sabin 1991, Schowalter *et al.* 1998, Seastedt 1984).

Microarthropods can increase or decrease rates of phosphorus mineralization, presumably as a result of their effect on microbial biomass (Seastedt 1984).

Calcium dynamics are highly variable. This element often is bound in organic acids (e.g., calcium oxalate) as well as in elemental and inorganic forms in detritus. Some fungi accumulate high concentrations of this element (Cromack *et al.* 1975, 1977, Schowalter *et al.* 1998), and some litter arthropods, especially millipedes and oribatid mites, have highly calcified exoskeletons (Norton and Behan-Pelletier 1991, Reichle *et al.* 1969). Nevertheless, calcium content in arthropod tissues is low compared to annual inputs in litter. No consistent arthropod effects on calcium mineralization have been apparent (Seastedt 1984).

Potassium and sodium are highly soluble elements, and their initial losses (via leaching) from decomposing litter invariably exceed mass losses (Schowalter and Sabin 1991, Schowalter *et al.* 1998, Seastedt 1984). Amounts of these elements entering the litter in precipitation or throughfall approach or exceed amounts entering as litterfall. In addition, these elements are not bound in organic molecules, so their supply in elemental form is adequate to meet the needs of microflora. Arthropods have been shown to affect mineralization of ^{134}Cs or ^{137}Cs, used as analogs of potassium (Crossley and Witkamp 1964, Witkamp and Crossley 1966), but not mineralization of potassium (Seastedt 1984). Sodium content often increases in decomposing litter, especially decomposing wood (Cromack *et al.* 1977, Schowalter *et al.* 1998). Sollins *et al.* (1987) suggested that this increase represented accumulation of arthropod tissues and products, which usually contain relatively high concentrations of sodium (e.g., Reichle *et al.* 1969). However, Schowalter *et al.* (1998) reported increased concentrations of sodium during early stages of wood decomposition, prior to sufficient accumulation of arthropod tissues. They suggested that increased sodium concentrations in wood reflected accumulation by decay fungi, which contained high concentrations of sodium in fruiting structures. Fungi and bacteria have no known physiological requirement for sodium (Cromack *et al.* 1977). Accumulation of sodium, and other limiting nutrients, in decomposing wood may represent a mechanism for attracting sodium-limited animals that transport fungi to new wood resources.

Sulfur accumulation in decomposing wood or forest and grassland soils (Schowalter *et al.* 1998, Stanko-Golden *et al.* 1994, Strickland and Fitzgerald 1986) reflects both physical adsorption of sulfate and biogenic formation of sulfonates by bacteria (Autry and Fitzgerald 1993). Although arthropods have no demonstrated role in these processes, arthropod feeding on bacterial groups responsible for sulfur mobilization or immobilization should influence sulfur dynamics. Because sulfur flux plays a major role in soil acidification and cation leaching, factors affecting sulfur immobilization require further investigation.

The generally insignificant effects of arthropods on net mineralization rates, compared to their substantial effects on mass loss, can be attributed to the compensatory effects of arthropods on microbial biomass. The stimulation by arthropods of microbial respiration and immobilization of nutrients results in loss of litter mass, especially carbon flux through respiration, but not of the standing crops of other elements within litter (Seastedt 1984). Other aspects of fragmentation also may contribute to nutrient retention, rather than loss. Aquatic comminuters generally fragment detritus into finer particles more amenable to downstream transport (J. Wallace and Webster 1996). However, some filter-feeders concentrate fine detrital material into larger fecal pellets that are more likely to remain in the aquatic ecosystem (e.g., Wotton *et al.* 1998). Some shredders deposit feces in burrows, thereby incorporating the nutrients into the substrate (R. Wagner 1991). Furthermore, Seastedt (2000) noted that most studies of terrestrial detritivore effects have been relatively short term. Accumulating data (e.g., Setälä *et al.* 1996) suggest that mixing of recalcitrant organic matter and mineral soil in the guts of some arthropods may produce stable soil aggregates that reduce the decay rate of organic material.

B. Soil Structure, Fertility, and Infiltration

Fossorial arthropods alter soil structure by redistributing soil and organic material and increasing soil porosity (J. Anderson 1988). Porosity determines the depth to which air and water penetrate the substrate. A variety of substrate-nesting vertebrates, colonial arthropods, and detritivorous arthropods and earthworms affect substrate structure, organic matter content, and infiltration in terrestrial and aquatic systems.

Defecation by a larval caddisfly, *Sericostoma personatum,* increases subsurface organic content in a stream ecosystem by 75–185% (R. Wagner 1991). The caddisfly feeds on detritus on the surface of the streambed at night and burrows into the streambed during the day, trapping organic matter in burrows.

Ants and termites are particularly important soil engineers. Colonies of these insects often occur at high densities and introduce cavities into large volumes of substrate. Eldridge (1993) reported that densities of funnel ant, *Aphaenogaster barbigula,* nest entrances could reach 37 m^{-2}, equivalent to 9% of the surface area over portions of the eastern Australian landscape. Nests of leaf-cutting ants, *Atta vollenweideri,* reach depths of >3 m in pastures in western Paraguay (Jonkman 1978). Moser (1963) partially excavated a leaf-cutting ant, *Atta texana,* nest in central Louisiana, United States. He found 93 fungus-garden chambers, 12 dormancy chambers, and 5 detritus chambers (for disposal of depleted foliage substrate) in a volume measuring 12 × 17 m on the surface by at least 4 m deep (the bottom of the colony could not be reached). Whitford *et al.* (1976) excavated nests of desert harvester ants, *Pogonomyrmex* spp., in New Mexico, United States, and mapped the 3-dimensional structure of interconnected chambers radiating from a central tunnel (Fig. 14.6). They reported colony densities of 21–23 ha^{-1} at 4 sites. Each colony consisted of 12–15 interconnected galleries (each about 0.035 m^3) within a 1.1 m^3 volume (1.5 m diameter × 2 m deep) of soil, equivalent to about 10 m^3 ha^{-1} cavity space (Fig. 14.6). These colonies frequently penetrated the calcified hardpan (caliche) layer 1.7–1.8 m below the surface.

The infusion of large soil volumes with galleries and tunnels greatly alters soil structure and chemistry. Termite and ant nests usually represent sites of concentrated organic matter and nutrients (J. Anderson 1988, Culver and Beattie 1983,

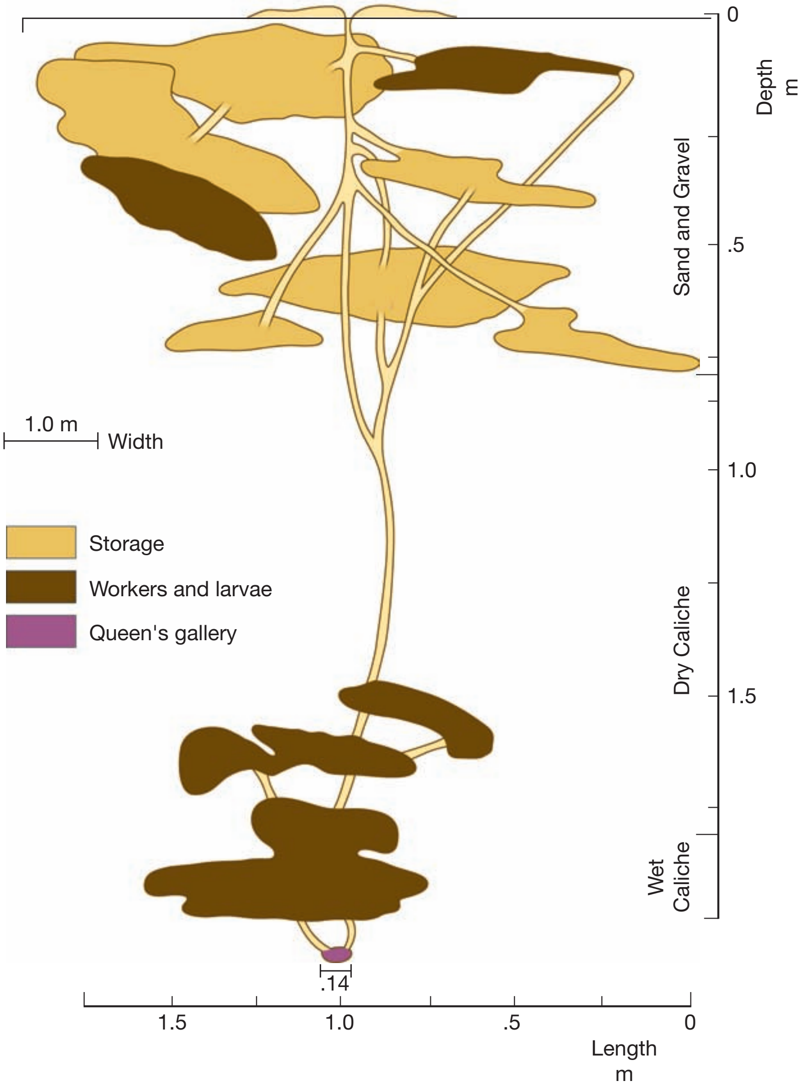


FIG. 14.6 Vertical structure of a harvester ant, *Pogonomyrmex rugosus,* nest in southern New Mexico. From Whitford *et al.* (1976) with permission of Birkhäuser Verlag.

Herzog *et al.* 1976, Holdo and McDowell 2004, J. Jones 1990, Lesica and Konnowski 1998, Mahaney *et al.* 1999, Salick *et al.* 1983, D. Wagner 1997, D. Wagner *et al.* 1997). Nests may have concentrations of macronutrients 2–3 times higher than surrounding soil (Fig. 14.7). J. Jones (1990) and Salick *et al.* (1983) noted that soils outside termite nest zones become relatively depleted of organic matter and nutrients. L. Parker *et al.* (1982) reported that experimental exclusion of termites for 4 years increased soil nitrogen concentration 11%. Ant nests also have been found to have higher rates of microbial activity and carbon and nitrogen mineralization than do surrounding soils (Dauber and Wolters 2000, Lenoir *et al.* 2001).

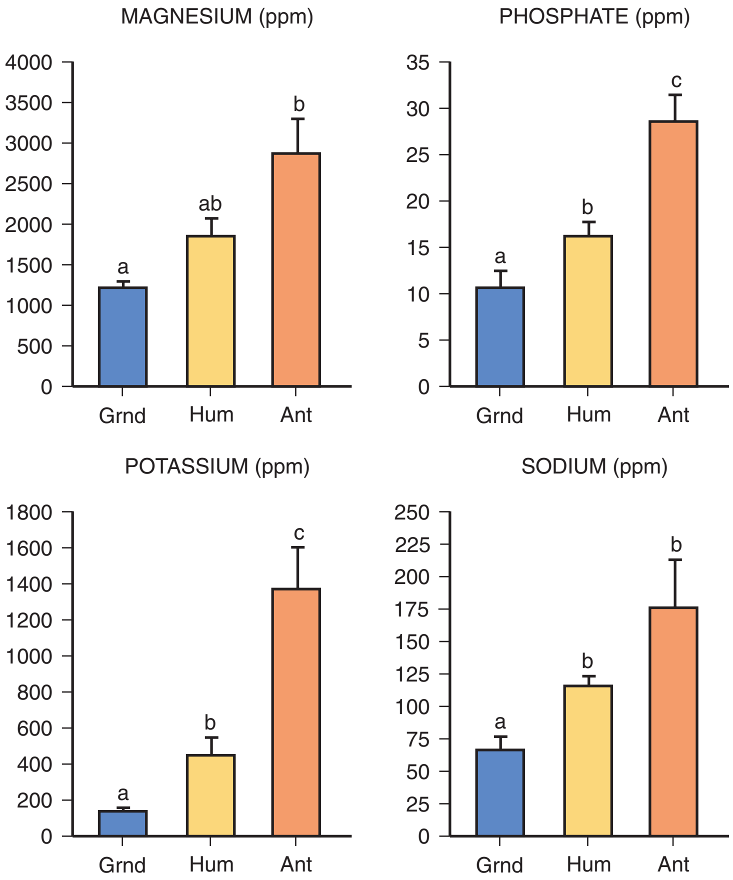


FIG. 14.7 Concentrations of major nutrients from bog soil (*Grnd*), hummocks (*Hum*), and *Formica* nests (*Ant*) in bogs in Montana, United States. Vertical bars represent 1 standard error. Means with different letters are significantly different at $P < 0.05$. From Lesica and Kannowski (1998) with permission from American Midland Naturalist. Please see extended permission list pg 573.

Nest pH often differs from surrounding soil. Mahaney *et al.* (1999) found significantly higher pH in termite mounds than in surrounding soils. Jonkman (1978) noted that soil within leaf-cutter ant, *Atta* spp., nests tended to have higher pH than did soil outside the nest. However, D. Wagner *et al.* (1997) measured significantly lower pH (6.1) in nests of harvester ants, *Pogonomyrmex barbatus,* than in reference soil (6.4). Lenoir *et al.* (2001) reported that *Formica rufa* nests had higher pH than did surrounding soil at one site and lower pH than did surrounding soil at a second site in Sweden. Ant mounds in Germany did not differ from surrounding soils (Dauber and Wolters 2000).

Termites and ants also transport large amounts of soil from lower horizons to the surface and above for construction of nests (Fig. 14.8), gallery tunnels, and "carton" (the soil deposited around litter material by termites for protection and to retain moisture during feeding above ground; Fig. 14.9) (Whitford 1986). Whitford *et al.* (1982) reported that termites brought 10–27 g m^{-2} of fine-textured

FIG. 14.8 Termite castle in northern Australian woodland. Dimensions are approximately 3 m height and 1.5 m diameter.

soil material (35% coarse sand; 45% medium fine sand; and 21% very fine sand, clay, and silt) to the surface and deposited 6–20 g of soil carton per gram of litter removed (see Fig. 14.3). Herrick and Lal (1996) found that termites deposited an average of 2.0 g of soil at the surface for every gram of dung removed. Mahaney *et al.* (1999) reported that the termite mound soil contained significantly more (20%) clay than did surrounding soils.

A variety of vertebrate species in Africa have been observed to selectively ingest termite mound soil. Mahaney *et al.* (1999) suggested that the higher clay content of termite mounds, along with higher pH and nutrient concentrations, could mitigate gastrointestinal ailments and explain termite soil consumption by chimpanzees. Termite mound soils, as well as surrounding soils, had high concentrations of metahalloysite, used pharmaceutically, and other clay minerals that showed mean binding capacities of 74–95% for 4 tested alkaloids. Chimpanzees could bind most of the dietary toxins present in 1–10 g of leaves by eating 100 mg of termite mound soil.

FIG. 14.9 Termite gallery carton on stems of dead creosote bush. Soil particles are cemented together to provide protection and moisture control during termite feeding on detrital material.

A number of studies have demonstrated effects of soil animals on soil moisture (Fig. 14.10). Litter reduction or removal increases soil temperature and evaporation and reduces infiltration of water. Burrowing and redistribution of soil and litter increase soil porosity, water infiltration, and stability of soil aggregates that control water- and nutrient-holding capacity.

Ant and termite nests have particularly important effects on soil moisture because of the large substrate surface areas and volumes affected. D. Wagner (1997) reported that soil near ant nests had higher moisture content than did more distant soil. Elkins *et al.* (1986) compared runoff and water infiltration in plots with termites present or excluded during the previous 4 years in New Mexico, United States. Plots with <10% plant cover had higher infiltration rates when termites were present (88 mm hour^{-1}) than when termites were absent (51 mm hour^{-1}); runoff volumes were twice as high in the termite-free plots with low plant cover (40 mm) as in untreated plots (20 mm). Infiltration and runoff

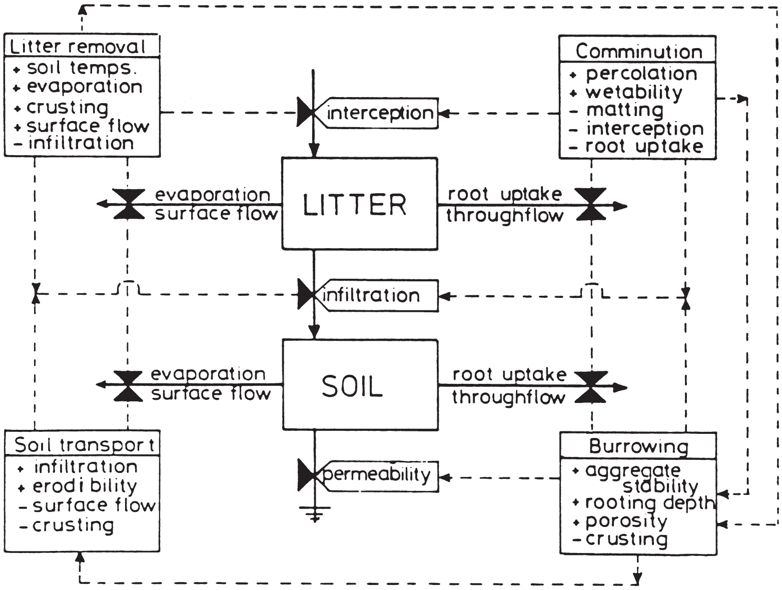


FIG. 14.10 Effects of soil invertebrates on soil water balance. From J. Anderson (1988) with permission from Elsevier Science.

volumes did not differ between shrub-dominated plots (higher vegetation cover) with or without termites.

Eldridge (1993, 1994) measured effects of funnel ants and subterranean harvester termites, *Drepanotermes* spp., on infiltration of water in semi-arid eastern Australia. He found that infiltration rates in soils with ant nest entrances were 4–10-fold higher (1030–1380 mm hour^{-1}) than in soils without nest entrances (120–340 mm-hour^{-1}). Infiltration rate was correlated positively with nest entrance diameter. However, infiltration rate on the subcircular pavements covering the surface over termite nests was an order of magnitude lower than in the annular zone surrounding the pavement or in interpavement soils (Fig. 14.11). The cemented surface of the pavement redistributed water and nutrients from the pavement to the surrounding annular zone. Ant and termite control of infiltration creates wetter microsites in moisture-limited environments.

C. Primary Production and Vegetation Dynamics

Through control of decomposition, mineralization, and pedogenesis, detritivorous and fossorial arthropods have the capacity to control nutrient availability for, and perhaps uptake by, plants (Crossley 1977). In particular, release of nitrogen from decaying organic matter often is correlated with plant productivity (Vitousek 1982). However, relatively few studies have measured the effect of detritivores and burrowers on plant growth or vegetation dynamics.

C. Edwards and Lofty (1978) compared seedling emergence and shoot and root growth of barley between pots of intact, sterilized soil (from fields in which seed had been either drilled into the soil or planted during ploughing) with

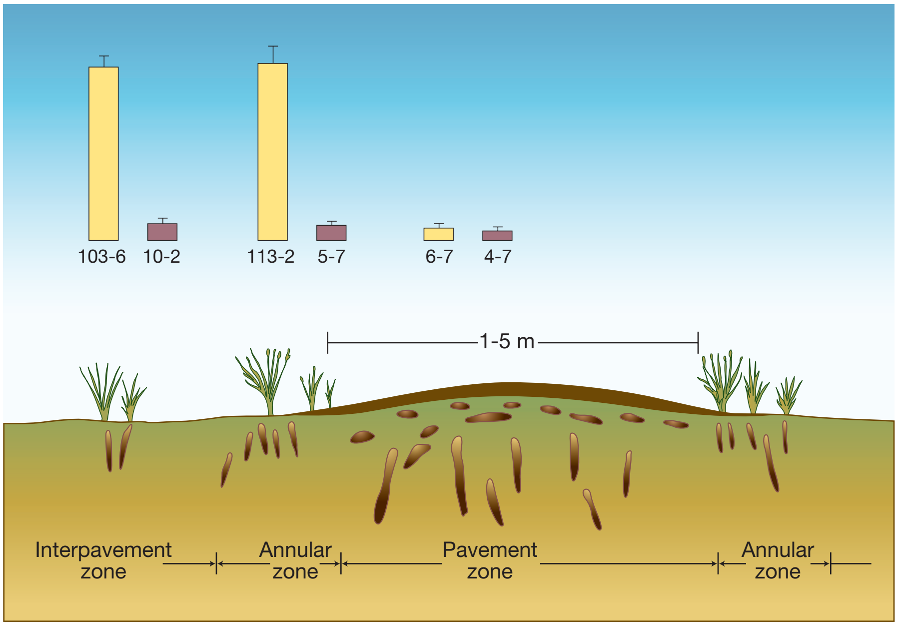


FIG. 14.11 Effect of termite colony structure on infiltration of water under ponded conditions (*yellow)* and under tension (*brown)*. Vertical lines indicate 1 standard error of the mean. From Eldridge (1994) with permission from Gustav Fischer Verlag.

microarthropods or earthworms absent or reintroduced. Percent seedling emergence, plant height, and root weight were higher in ploughed soil and direct-drilled soil with animals, compared to sterile direct-drilled soil, suggesting important effects of soil animals on mineralization, soil porosity, and infiltration.

R. Ingham *et al.* (1985) inoculated microcosms of blue grama grass, *Bouteloua gracilis,* in sandy loam soil, low in inorganic nitrogen, inoculated with bacteria or fungi; half of each microflora treatment was inoculated with microbivorous nematodes. Plants growing in soil with bacteria and bacteriophagous nematodes grew faster and acquired more nitrogen initially than did plants in soil with bacteria only. Addition of mycophagous nematodes did not increase plant growth. These differences in plant growth resulted from greater nitrogen mineralization by bacteria (compared to fungi), excretion of NH_4^+-N by bacteriophagous (but not mycophagous) nematodes, and rapid uptake of available nitrogen by plants. Mycophagous nematodes did not increase plant growth or nitrogen uptake over fungi alone because these nematodes excreted less NH_4^+-N, and the fungus alone mineralized sufficient nitrogen for plant growth.

In a unique, definitive study, Setälä and Huhta (1991) created laboratory microcosms with birch seedlings, *Betula pendula,* planted in partially sterilized soil reinoculated with soil microorganisms only or with soil microorganisms and a diverse soil fauna. During 2 growing periods the presence of soil fauna increased birch leaf, stem, and root biomass by 70%, 53%, and 38%, respectively, and increased foliar nitrogen and phosphorus contents 3-fold and 1.5-fold, respectively, compared to controls with microorganisms only (Fig. 14.12).

In addition to direct effects on nutrient availability, soil arthropods can influence plant growth indirectly by affecting mycorrhizal fungi. Grazing on mycorrhizal fungi by fungivorous arthropods could inhibit plant growth by interfering with nutrient uptake. Conversely, many fungivorous arthropods disperse mycorrhizal spores or hyphae to new hosts. Rabatin and Stinner (1988) reported that 28–97% of soil animals contained mycorrhizal spores or hyphae in their guts.

Soil animals also influence vegetation dynamics. Several studies have demonstrated that ant and termite mounds usually support distinct plant communities (Garrettson *et al.* 1998, Guo 1998, Holdo and McDowell 2004, King 1977a). Guo (1998) reported that the diversity of annual and perennial plants was highest on ant mounds and under shrubs, compared to kangaroo rat mound, half-shrub, and open-area microsites; biomass of these plants was highest under shrubs, followed

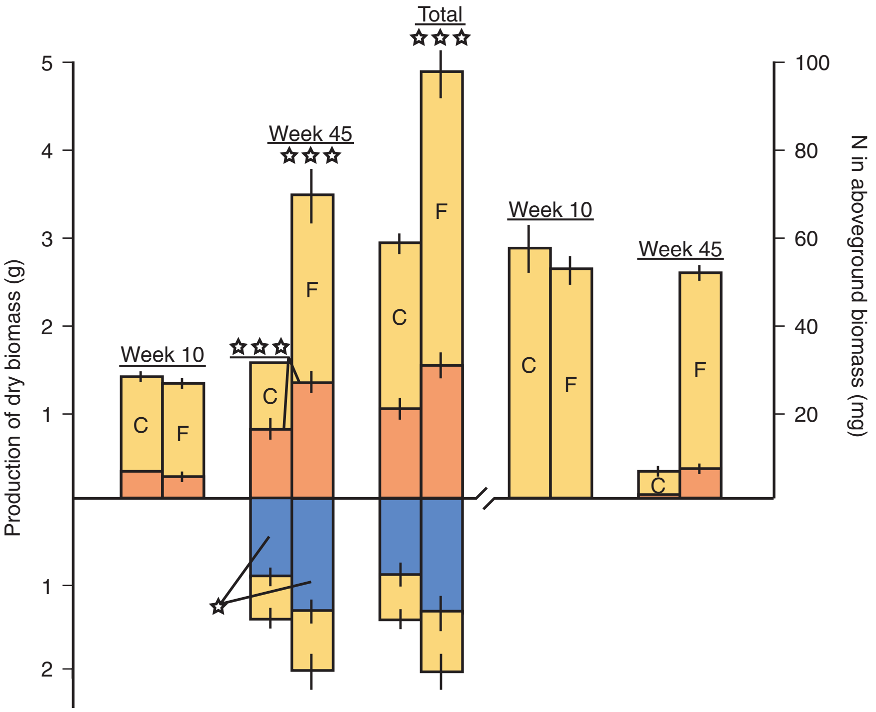


FIG. 14.12 Biomass production (*left of break in horizontal axis)* and nitrogen accumulation (*right of break in horizontal axis)* of birch, *Betula pendula,* seedlings. Bars above the horizontal axis are stems (*orange)* and leaves (*yellow)*; bars below the horizontal axis are roots in humus (*blue)* and roots in mineral soil (*yellow)*. C, fauna removed; F, refaunated. Vertical lines represent 1 standard deviation for all data (except nitrogen at week 45, where vertical lines represent minimum and maximum values). (For C versus F, *, $P < 0.05$; ***, $P < 0.001$). Stem nitrogen was not measured week 10. From Setälä and Huhta (1991) with permission from the Ecological Society of America.

by kangaroo rat mounds and ant mounds, indicating that ant mounds are important determinants of vegetation structure.

Jonkman (1978) reported that abandoned nests of leaf-cutter ants, *Atta vollenweideri,* served as sites of accelerated succession in Paraguayan pastures. Collapse of the nest chamber formed a depression that held water and facilitated development of woody vegetation. At high nest densities, these oases coalesced, greatly increasing forest area. Brenner and Silva (1995) found that active nests of *Atta laevigata* were more frequently associated with groves of trees, and the size of nests increased with grove size and the abundance of forest tree species in Venezuelan savanna, suggesting that active nests both facilitated and were facilitated by formation of groves.

L. Parker *et al.* (1982) demonstrated that termite exclusion significantly reduced biomass of four annual plant species and significantly increased biomass of one annual plant species. They observed an overall trend toward increased biomass of annual plants in plots with termites excluded. These results likely reflected increased nitrogen availability in termite exclusion plots, compared to plots with unmanipulated termite abundance.

Lesica and Kannowski (1998) reported that wood ants, *Formica podzolica,* were responsible for mound formation in peat bogs in Montana, United States. The mounds provided elevated habitat that was warmer, was better aerated, and had higher nutrient content than did surrounding peat surfaces (see Fig. 14.7). Although active mounds supported only a few species of grasses, abandoned nests supported shrubs and plant species that could not grow in the saturated peat surface. The ants foraged primarily on honeydew from aphids tended on shrubs, indicating a positive feedback relationship.

The high nutrient concentrations of termite and ant nests are incorporated by plants growing on the nests and become available to higher trophic levels. Holdo and McDowell (2004) reported that trees growing on termite mounds had higher concentrations of all nutrients tested, except sodium and crude protein, than were trees from the surrounding woodland matrix in Zimbabwe. Trees on mounds also were subjected to more intense feeding by elephants. Termite and ant nests thereby affect food availability and feeding patterns for herbivores, providing indirect positive feedback for herbivore effects on litter quality and availability for detritivores.

III. SUMMARY

Decomposition and pedogenesis are major ecosystem processes that affect biogeochemical cycling, trace gas fluxes, soil fertility, and primary production. Decomposition of organic matter involves four component processes: photooxidation, leaching, comminution, and mineralization. Arthropods are key factors influencing comminution and mineralization.

Functional groups involved in decomposition include coarse comminuters that fragment large materials and fine comminuters that fragment smaller materials, often those produced by large comminuters. In aquatic ecosystems, scrapers and shredders represent coarse comminuters, whereas gatherers and filterers represent fine comminuters. Xylophages represent a specialized group of comminuters that fragment woody litter. Carrion feeders reduce carcasses, and coprophages feed on animal excrement. Fungivores and bacteriovores fragment detrital material while grazing on microflora. Fossorial functional groups include subterranean nesters that excavate simple burrows; gatherers that return detrital or other organic materials to nesting areas; and fossorial feeders that consume organic material, soil, or both and mix biotic and abiotic materials in their wake.

Evaluation of detritivore and burrower effects on decomposition and pedogenesis requires appropriate methods for measuring animal abundances and process rates. Abundances of detritivores or burrowers can be manipulated using exclusion and microcosm techniques, and detritivory can be measured as the product of detritivore abundance and individual consumption rate or as the rate of disappearance of substrate. Decomposition most commonly is measured as respiration rate, as the ratio of litter input to litter standing crop, or as the rate of litter disappearance. Isotopic tracers also provide data on decomposition rate.

Decomposition rate usually is higher in mesic than in arid ecosystems. Different functional groups dominate different ecosystems, depending on availability and quality of detrital resources. For example, shredders dominate headwater streams where coarse detrital inputs are the primary resource, whereas filterers dominate larger streams with greater availability of suspended fine organic material. Xylophages occur only in ecosystems with woody residues. Decomposition generally can be modeled as a multiple negative exponential decay function over time, with decay constants proportional to the quality of litter components. Usually, an initial large decay constant represents rapid loss of labile materials and successively smaller decay constants represent slower losses of recalcitrant materials (e.g., lignin and cellulose). Most studies have been relatively short term. Recent long-term studies suggest that mixing of recalcitrant materials and soil in arthropod guts may create stable aggregates that decay very slowly.

Detritivores affect decomposition in three ways: through comminution, effects on microbial biomass, and effects on mineralization. Comminution increases detrital surface area and facilitates colonization and decay by microflora. Low to moderate levels of grazing on microflora stimulate microbial productivity and biomass, maximizing microbial activity and respiration. High levels of grazing may reduce microbial biomass and decomposition. Grazers also disperse fungi and bacteria to new substrates. Not all organic material is converted to CO_2. The low oxygen concentrations characterizing warm, humid termite colonies favor reduction of organic molecules to methane and other trace gases. Arthropod detritivores affect mineralization in different ways, depending on the chemical characteristics and biological use of the element. Detritivores often increase mineralization of nitrogen, but nitrogen released from detritus may be immobilized quickly by microorganisms.

Burrowers affect soil development by redistributing soil and organic matter. Ants and termites, in particular, excavate large volumes of soil and accumulate organic material in their centralized nests, mixing soil with organic material and influencing the distribution of soil nutrients and organic matter. Surrounding soils may become depleted in soil carbon and nutrients.

Detritivore and burrower effects on mineralization and soil composition can affect primary production and vegetation dynamics. Elevated moisture and nutrient concentrations in, or adjacent to, ant and termite nests support distinct vegetation and may facilitate succession following colony abandonment. A few studies have demonstrated increased plant growth, altered vegetation structure, and increased herbivory resulting from detritivore-induced nutrient mobilization.

15

Insects as Regulators of Ecosystem Processes

INSECTS, AND OTHER ORGANISMS, INEVITABLY AFFECT THEIR ENVIRONMENT through spatial and temporal patterns of resource acquisition and redistribution. Insects respond to environmental changes in ways that dramatically alter ecosystem conditions, as discussed in Chapters 12–14. These effects of organisms do not necessarily provide cybernetic (stabilizing) regulation. However, the hypothesis that insects stabilize ecosystem properties through feedback regulation is one of the most important and revolutionary concepts to emerge from research on insect ecology and should be considered in making pest management decisions in natural ecosystems.

The concept of self-regulation is a key aspect of ecosystem ecology. Vegetation has a documented role in ameliorating variation in climate and biogeochemical cycling (Chapter 11), and vegetative succession facilitates recovery of ecosystem functions following disturbances. However, the concept of self-regulating ecosystems has seemed to be inconsistent with evolutionary theory (emphasizing selection of "selfish" attributes) (e.g., Pianka 1974), with variable successional trends following disturbance (e.g., H. Horn 1981) and with the lack of obvious mechanisms for maintaining homeostasis (e.g., Engelberg and Boyarsky 1979).

The debate over the self-regulating capacity of ecosystems, and especially the role of insects, is somewhat reminiscent of debate on the now-recognized importance of density-dependent feedback regulation of population size (Chapter 16) and is a useful example of how science develops. The outcome of this debate has significant consequences for how we manage ecosystems and their biotic resources. Although controversial, this concept is an important aspect of insect ecology, and its major issues are the subject of this chapter.

I. DEVELOPMENT OF THE CONCEPT

The intellectual roots of ecosystem self-regulation lie in Darwin's (1859) recognition that some adaptations apparently benefit a group of organisms more than the individual, leading to selection for population stability. The concept of altruism and selection for homeostasis at supraorganismal levels has remained an important issue, despite recurring challenges and alternative models (e.g., Axelrod and Hamilton 1981, Schowalter 1981, E. Wilson 1973, 1997).

Behavioral ecologists have been challenged to explain the evolution of altruistic behaviors that are fundamental to social organization. Even sexual reproduction could be considered a form of self-restraint because individuals contribute only half the genotype of their progeny through sexual reproduction, compared to the entire genotype of their progeny through asexual reproduction (Pianka 1974). Cooperative interactions, such as mutualism, and self-sacrificing behavior, such as suppression of reproduction and suicidal defense by workers of social insects, have been more difficult to explain in terms of individual selection. Haldane (1932) proposed a model in which altruism would have a selective advantage if the starting gene frequency were high enough and the benefits to the group outweighed individual disadvantage. This model raised obvious questions about the origin of altruist genes and the relative advantages and disadvantages that would be necessary for increased frequency of altruist genes.

Group selection theory was advanced during the early 1960s by Wynne-Edwards (1963, 1965), who proposed that social behavior arose as individuals evolved to curtail their own individual fitnesses to enhance survival of the group. Populations that do not restrain combat among their members or that overexploit their resources have a higher probability of extinction than do populations that regulate combat or resource use. Selection thus should favor demes with traits to regulate their densities (i.e., maintain homeostasis in group size). Behaviors such as territoriality, restraint in conflict, and suppressed reproduction by subordinate individuals (including workers in social insect colonies) thereby reflect selection (feedback) for traits that prevent destructive interactions or oscillations in group size.

This hypothesis was challenged for lack of explicit evolutionary models or experimental tests that could explain the progressive evolution of homeostasis at the group level (i.e., demonstration of an individual advantage to altruistic individuals over selfish individuals). Furthermore, Wynne-Edwards' proposed devices by which individuals curtail their individual fitnesses, and communicate their density and the degree to which each individual should decrease its individual fitness, were inconsistent with available evidence or could be explained better by models of individual fitness (E. Wilson 1973). Nevertheless, the concept of group selection was recognized as an important aspect of social evolution (E. Wilson 1973). Hamilton (1964) and J. M. Smith (1964) developed an evolutionary model, based on *kin selection,* whereby individual fitness is increased by behaviors that favor survival of relatives with similar genotypes. They introduced a new term, *inclusive fitness,* to describe the contributions of both personal reproduction and reproduction by near kin to individual fitness. For example, care for offspring of one's siblings increases an individual's fitness to the extent that it contributes to the survival of related genotypes. Failure to provide sufficient care for offspring of siblings reduces survival of family members.

This concept explained evolution of altruistic behaviors, such as maternal care; shared rearing of offspring among related individuals; alarm calls (that may draw attention of predators to the caller); and voluntary suppression of reproduction and suicidal defense by workers in colonies of social insects, which usually benefit close relatives. For social Hymenoptera, Hamilton (1964) noted that males are produced from unfertilized eggs and have unpaired chromosomes. Accordingly, all the daughters in the colony inherit only one type of gamete from their father and thereby share 50% of their genes through this source. In addition, they share another 25%, on average, of their genes in common from their mother. Overall, the daughters share 75% of their genes with each other compared to only 50% of their genes with their mother. Therefore, workers maximize their fitness by helping to rear siblings, rather than by having their own offspring.

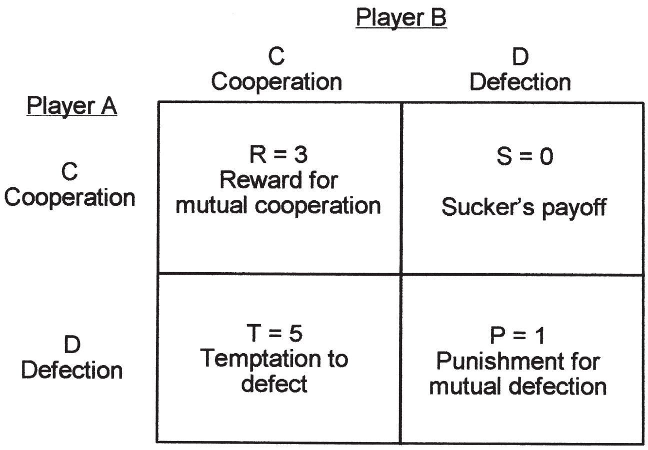
This model does not apply to termites. Husseneder *et al.* (1999) and Thorne (1997) suggested that developmental and ecological factors, such as slow development, iteroparity, overlap of generations, food-rich environment, high risk of dispersal, and group defense, may be more important than genetics in the maintenance of termite eusociality, whatever factors may have favored its original development.

Levins (1970) and Boorman and Levitt (1972) proposed *interdemic selection* models to account for differential extinction rates among demes of metapopulations that differ in altruistic traits. In the Levins model, colonists from small populations found other small populations in habitable sites. Increasing frequency of altruist genes decreases the probability of extinction of these small populations (i.e., cooperation elevates and maintains each deme above the extinction threshold; see Chapters 6 and 7). In the Boorman–Levitt model, colonists from a large, stable population found small, marginal populations in satellite habitats. Altruist genes do not influence extinction rates until marginal populations reach demographic carrying capacity (i.e., altruism prevents destructive population increase above carrying capacity; see Chapters 6 and 7). Both models require restrictive conditions for evolution of altruist genes. Matthews and Matthews (1978) noted that group selection requires that an allele become established by selection at the individual level. Thereafter, selection could favor demes with altruist genes that reduce extinction rates, relative to demes without these genes. Interdemic selection has become a central theme in developing concepts of metapopulation dynamics (Chapter 7).

Meanwhile, the concept of group selection was implicit in early models of ecological succession and community development. The facilitation model of succession proposed by Clements (1916) and elaborated by E. Odum (1953, 1969) emphasized the apparently progressive development of a stable, "climax," ecosystem through succession. Each successional stage altered conditions in ways that benefited the replacing species more than itself. However, such facilitation contradicted individual self-interest that was fundamental to the theory of natural selection. Furthermore, identification of alternative models of succession, including the inhibition model (Chapter 10), made succession appear to be more consistent with evolutionary theory.

D. S. Wilson (1976, 1997) developed a model that specifically applied the concept of group selection to the community level. Wilson recognized that individuals and species affect their own fitness through effects on their environment, including the fitness of other individuals. For example, earthworm effects on soil development stimulate plant growth, herbivory, and litter production (see Chapter 14) and thereby increase the detrital resources exploited by the worms, a positive feedback. Furthermore, spatial heterogeneity, from large geographic to microsite scales, in population distribution results in intrademic variation in effects of organisms on their community. Given sufficient iterations of Wilson's model, every effect of a species on its community eventually affects that species, positively or negatively, through all possible feedback pathways. Intrademic variation in effects on the environment is subject to selection for adaptive traits of individuals.

The models described earlier in this section help explain the increased frequency of altruist genes, but what selective factors can maintain altruist genes in the face of evolutionary pressure to "cheat" among nonrelated individuals? Trivers (1971) and Axelrod and Hamilton (1981) developed a model of *reciprocal altruism* based on the Prisoner's Dilemma (Fig. 15.1), in which each of two players can cooperate or defect. Each player can choose to cooperate or defect if the other player chooses to cooperate or defect. If the first player acts cooperatively, the benefit/cost for cooperation by the second player (reward for mutual cooperation) is less than that for defection (temptation for the first player



	Player B	
Player A	C Cooperation	D Defection
C Cooperation	R = 3 Reward for mutual cooperation	S = 0 Sucker's payoff
D Defection	T = 5 Temptation to defect	P = 1 Punishment for mutual defection

FIG. 15.1 Prisoner's Dilemma, defined by $T > R > P > S$ and $R > (S + T)/2$, with payoff to player A shown using illustrative values. From Axelrod and Hamilton (1981) with permission from the American Association for the Advancement of Science. Please see extended permission list pg 573.

to defect in the future); if the first player defects, the benefit/cost for cooperation by the second player (sucker's payoff) is less than that for defection (punishment for mutual defection). Therefore, if the interaction occurs only once, defection (noncooperation) is always the optimal strategy, despite both individuals doing worse than they would if they both cooperate. However, Axelrod and Hamilton (1981) recognized the probability of repeated interaction between pairs of unrelated individuals and addressed the initial viability (as well as final stability) of cooperative strategies in environments dominated by noncooperating individuals or more heterogeneous environments composed of other individuals using a variety of strategies. After numerous computer simulations with a variety of strategies, they concluded that the most robust strategy in an environment of multiple strategies also was the simplest, *Tit-for-Tat.* This strategy involves cooperation based on reciprocity and a memory extending only one move back (i.e., never being the first to defect but retaliating after a defection by the other and forgiving after just one act of retaliation). They also found that once Tit-for-Tat was established, it resisted invasion by possible mutant strategies as long as the interacting individuals had a sufficiently large probability of meeting again.

Axelrod and Hamilton emphasized that Tit-for-Tat is not the only strategy that can be evolutionarily stable. The *Always Defect Strategy* also is evolutionarily stable, no matter what the probability of future interaction. They postulated that altruism could appear between close relatives, when each individual has part interest in the partner's gain (i.e., rewards in terms of inclusive fitness), whether or not the partner cooperated. Once the altruist gene exists, selection would favor strategies that base cooperative behavior on recognition of cues, such as relatedness or previous reciprocal cooperation. Therefore, individuals in relatively stable environments are more likely to experience repeated interaction and selection for reciprocal cooperation than are individuals in unstable environments that provide low probabilities of future interaction.

These models demonstrate that selection at supraorganismal levels must be viewed as contributing to the inclusive fitness of individuals. Cooperating individuals have demonstrated greater ability in finding or exploiting uncommon or aggregated resources, defending shared resources, and mutual protection (Hamilton 1964). Cooperating predators (e.g., wolves and ants) have higher capture efficiency and can acquire larger prey compared to solitary predators. The mass attack behavior of bark beetles is critical to successful colonization of living trees. Co-existing caddisfly larvae can modify substrate conditions and near-surface water velocity, thereby enhancing food delivery (Cardinale *et al.* 2002). Animals in groups are more difficult for predators to attack.

Reciprocal cooperation reflects selection via feedback from individual effects on their environment. The strength of individual effects on the environment is greatest among directly interacting individuals and declines from the population to community levels (Fig. 1.2) (e.g., Lewinsohn and Price 1996). Reciprocal cooperation can explain the evolution of sexual reproduction and social behavior as the net result of tradeoffs between maximizing the contribution of an individual's own genes to its progeny and maximizing the contribution of genes represented in the individual to progeny of its relatives. Similarly, species interactions represent tradeoffs among positive and negative effects (see Chapter 8).

Population distribution in time and space (i.e., metapopulation dynamics; see Chapter 7) is a major factor affecting interaction strengths. Individuals dispersed in a regular pattern (Chapter 5) over an area will affect a large proportion of the total habitat and interact widely with co-occurring populations, whereas the same total number of individuals dispersed in an aggregated pattern will affect a smaller proportion of the total habitat but may have a higher frequency of interactions with co-occurring populations in areas of local abundance. Consistency of population dispersion through time affects the long-term frequency of interactions and reinforcement of selection from generation to generation. Metapopulation dynamics interacting with disturbance dynamics provide the template for selection of species assemblages best adapted to local environmental variation.

II. ECOSYSTEMS AS CYBERNETIC SYSTEMS

The cybernetic nature of ecosystems, from patch to global scales, has been a central theme of ecosystem ecology. J. Lovelock (1988) suggested that autotroph–heterotroph interactions have been responsible for the development and regulation of atmospheric composition and climate that are suitable for the persistence of life. The ability of ecosystems to minimize variability in climate and rates of energy and nutrient fluxes would affect responses to anthropogenic changes in global conditions.

A. Properties of Cybernetic Systems

Cybernetic systems generally are characterized by (1) information systems that integrate system components, (2) low-energy feedback regulators that have high-energy effects, and (3) goal-directed stabilization of high-energy processes. Mechanisms that sense deviation (perturbation) in system condition communicate with mechanisms that function to reduce the amplitude and period of deviation. Negative feedback is the most commonly recognized method for stabilizing outputs. A thermostat represents a simple example of a negative feedback mechanism. The thermostat senses a departure in room temperature from a set level and communicates with a temperature control system that interacts with the thermostat to readjust temperature to the set level. The room system is maintained at temperatures within a narrow equilibrial range.

Organisms are recognized as cybernetic systems with neurological networks for communicating physiological conditions and various feedback loops for maintaining homeostasis of biological functions. Cybernetic function is perhaps best developed among homeotherms. These organisms are capable of self-regulating internal temperature through physiological mechanisms that sense change in body temperature and trigger changes in metabolic rate, blood flow, and sweat that increase or decrease temperature as necessary. However, energy demand is high for such regulation. Heterotherms also have physiological and behavioral mechanisms for adjusting body temperature within a somewhat wider range but with lower energy demand (see Chapters 2 and 4). Regardless of mechanism, the result is sufficient stability of metabolic processes for survival.

Although self-adjusting mechanical systems and organisms are the best-recognized examples of cybernetic systems, the properties of self-regulating systems have analogs at supraorganismal levels (B. Patten and Odum 1981, Schowalter 1985, 2000). Human families and societies express goals in terms of survival, economic growth, improved living conditions, and so on and accomplish these goals culturally through governing bodies, communication networks, and balances between reciprocal cooperation (e.g., trade agreements, treaties) and negative feedback (e.g., economic regulations, warfare).

B. Ecosystem Homeostasis

E. Odum (1969) presented a number of testable hypotheses concerning ecosystem capacity to develop and maintain homeostasis, in terms of energy flow and biogeochemical cycling, during succession. Although subsequent research has shown that many of the predicted trends are not observed, at least in some ecosystems, Odum's hypotheses focused debate on ecosystems as cybernetic systems. Engelberg and Boyarsky (1979) argued that ecosystems do not possess the critical goal-directed communication and low-cost/large-effect feedback systems required of cybernetic systems. Although ecosystems can be shown to possess these properties of cybernetic ecosystems, as described later in this section, this debate cannot be resolved until ecosystem ecologists reach consensus on a definition and measurable criteria of stability and demonstrate that potential homeostatic mechanisms, such as biodiversity and insects (see later in this chapter), function to reduce variability in ecosystem conditions.

Although discussion of ecosystem goals appears to be teleological, nonteleological goals can be identified (e.g., maximizing distance from thermodynamic ground; see B. Patten 1995, a requisite for all life). Stabilizing ecosystem conditions obviously would reduce exposure of individuals and populations to extreme, and potentially lethal, departures from normal conditions. Furthermore, stable population sizes would prevent extreme fluctuations in abundances that would jeopardize stability of other variables. Hence, environmental heterogeneity might select for individual traits that contribute to stability of the ecosystem.

The argument that ecosystems do not possess centralized mechanisms for communicating departure in system condition and initiating responses (e.g., Engelberg and Boyarsky 1979) ignores the pervasive communication network in ecosystems (see Chapters 2, 3, and 8). However, the importance of volatile chemicals for communicating resource conditions among species has been recognized relatively recently (Baldwin and Schultz 1983, Rhoades 1983, Sticher *et al.* 1997, Turlings *et al.* 1990, Zeringue 1987). The airstream carries a blend of volatile chemicals, produced by the various members of the community, that advertises the abundance, distribution, and condition of various organisms within the community. Changes in the chemical composition of the local atmosphere indicate changes in the relative abundance and suitability of hosts or the presence and proximity of competitors and predators. Sensitivity among organisms to the chemical composition of the atmosphere or water column may provide a global information network that communicates conditions for a variety of populations and initiates feedback responses.

Feedback loops are the primary mechanisms for maintaining ecosystem stability, regulating abundances and interaction strengths (W. Carson and Root 2000, de Ruiter *et al.* 1995, B. Patten and Odum 1981, Polis *et al.* 1997a, b, 1998). The combination of bottom-up (resource availability), top-down (predation), and lateral (competitive) interactions generally represent negative feedback, stabilizing food webs by reducing the probability that populations increase to levels that threaten their resources (and, thereby, other species supported by those resources). Mutualistic interactions and other positive feedbacks reduce the probability of population decline to extinction thresholds. Although positive feedback often is viewed as destabilizing, such feedback may be most important when populations are small and likely is limited by negative feedbacks as populations grow beyond threshold sizes (Ulanowicz 1995). Such compensatory interactions may maintain ecosystem properties within relatively narrow ranges, despite spatial and temporal variation in abiotic conditions (Kratz *et al.* 1995, Ulanowicz 1995). Omnivory increases ecosystem stability, perhaps by increasing the number of linkages subject to feedback (Fagan 1997). Ecological succession represents one mechanism for recovery of ecosystem properties following disturbance-induced departures from nominal conditions.

The concept of self-regulation does not require efficient feedback by all ecosystems or ecosystem components. Just as some organisms (recognized as cybernetic systems) have greater homeostatic ability than do others (e.g., homeotherms vs. heterotherms), some ecosystems demonstrate greater homeostatic ability than do others (J. Webster *et al.* 1975). Frequently disturbed ecosystems may be reestablished by relatively random assemblages of opportunistic colonists and select genes for rapid exploitation and dispersal. Their short duration provides little opportunity for repeated interaction that could lead to stabilizing cooperation (cf. Axelrod and Hamilton 1981). Some species increase variability or promote disturbance (e.g., brittle or flammable species; e.g., easily toppled *Cecropia* and flammable *Eucalyptus*). Insect outbreaks increase variation in some ecosystem parameters (Romme *et al.* 1986), often in ways that promote regeneration of resources (e.g., Schowalter *et al.* 1981a). Despite this, relatively stable environments, such as tropical rainforests, might not select for stabilizing interactions. However, stable environmental conditions should favor consistent species interactions and the evolution of reciprocal cooperation, such as demonstrated by a diversity of mutualistic interactions in tropical forests. Selection for stabilizing interactions should be greatest in ecosystems characterized by intermediate levels of environmental variation. Interactions that reduce such variation would contribute to individual fitnesses.

C. Definition of Stability

B. Patten and Odum (1981) proposed that a number of time-invariant or regularly oscillating ecosystem parameters represent potential goals for stabilization. These included total system production (P) and respiration (R), P : R ratio, total chlorophyll, total biomass, nutrient pool sizes, species diversity, population sizes, etc. However, the degree of spatial and temporal variability of these parameters remains poorly known for most, even intensively studied, ecosystems (Kratz *et al.* 1995).

Kratz *et al.* (1995) compiled data on the variability of climatic, edaphic, plant, and animal variables from 12 Long Term Ecological Research (LTER) sites, representing forest, grassland, desert, lotic, and lacustrine ecosystems in the United States. Unfortunately, given the common long-term goals of these projects, comparison was limited because different variables and measurement techniques were represented among these sites. Nevertheless, Kratz *et al.* offered several important conclusions concerning variability.

First, the level of species combination (e.g., species, family, guild, total plants or animals) had a greater effect on observed variability in community structure than did spatial or temporal extent of data. For plant parameters, species- and guild-level data were more variable than were data for total plants; for animal parameters, species-level data were more variable than were guild-level data, and both were more variable than were total animal data. As discussed for food-web properties in Chapter 9, the tendency to ignore diversity, especially of insects (albeit for logistic reasons), clearly affects our perception of variability. Detection of long-term trends or spatial patterns depends on data collection for parameters sufficiently sensitive to show significant differences but not so sensitive that their variability hinders detection of differences.

Second, spatial variability exceeded temporal variability. This result indicates that individual sites are inadequate to describe the range of variation among ecosystems within a landscape. Variability must be examined over larger spatial scales. Edaphic data were more variable than were climatic data, indicating high spatial variation in substrate properties, whereas common weather across landscapes homogenizes microclimatic conditions. This result also could be explained as the result of greater biotic modification of climatic variables compared to substrate variables (see the following text).

Third, biotic data were more variable than were climatic or edaphic data. Organisms can exhibit exponential responses to incremental changes in abiotic conditions (see Chapter 6). The ability of animals to move and alter their spatial distribution quickly in response to environmental changes is reflected in greater variation in animal data compared to plant data. However, animals also have greater ability to hide or escape sampling devices.

Finally, two sites, a desert and a lake, provided a sufficiently complete array of biotic and abiotic variables to permit comparison. These two ecosystem types represent contrasting properties. Deserts are exposed to highly variable and harsh abiotic conditions but are interconnected within landscapes, whereas lakes exhibit relatively constant abiotic conditions (buffered from thermal change by mass and latent heat capacity of water, from pH change by bicarbonates, and from biological invasions by their isolation) but are isolated by land barriers. Comparison of variability between these contrasting ecosystems supported the hypothesis that deserts are more variable than lakes among years, but lakes are more variable than deserts among sites.

Kratz *et al.* (1995) provided important data on variation in a number of ecosystem parameters among ecosystem types. However, important questions remain. Which parameters are most important for stability? How much deviation can be tolerated? What temporal and spatial scales are relevant to ecosystem stability?

Among the parameters that could be stabilized as a result of species interactions, net primary production (NPP) and biomass structure (living and dead) may be particularly important. Many other parameters, including energy, water and nutrient fluxes, trophic interactions, species diversity, population sizes, climate, and soil development, are directly or indirectly determined by NPP or biomass structure (Boulton *et al.* 1992; see Chapter 11). In particular, the ability of ecosystems to modify internal microclimate, protect and modify soils, and provide stable resource bases for primary and secondary producers depends on NPP and biomass structure. Therefore, natural selection over long periods of co-evolution should favor individuals whose interactions stabilize these ecosystem parameters. NPP may be stabilized over long time periods as a result of compensatory community dynamics and biological interactions, such as those resulting from biodiversity and herbivory (see later in this chapter).

No studies have addressed the limits of deviation, for any parameter, within which ecosystems can be regarded as qualitatively stable. Traditional views of stability have emphasized consistent species composition, at the local scale, but shifts in species composition may be a mechanism for maintaining stability in other ecosystem parameters, at the landscape or watershed scale. This obviously is an important issue for evaluating stability and predicting effects of global environmental changes. However, given the variety of ecosystem parameters and their integration at the global scale, this issue will be difficult to resolve.

The range of parameter values within which ecosystems are conditionally stable may be related to characteristic fluctuations in environmental conditions or nutrient fluxes. For example, biomass accumulation increases ecosystem storage capacity and ability to resist variation in resource availability (J. Webster *et al.* 1975) but also increases ecosystem vulnerability to some disturbances, including fire and storms. Complex ecosystems with high storage capacity (i.e., forests) are the most buffered ecosystems, in terms of regulation of internal climate, soil conditions, and resource supply, but also fuel the most catastrophic fires under drought conditions and suffer the greatest damage during cyclonic storms. Hence, ecosystems with lower biomass, but rapid turnover of matter or nutrients, may be more stable under some environmental conditions. Species interactions that periodically increase rates of nutrient fluxes and reduce biomass (e.g., herbivore outbreaks) traditionally have been viewed as evidence of instability but may contribute to stability of ecosystems in which biomass accumulation or rates of nutrient turnover from detritus are destabilizing (de Mazancourt *et al.* 1998, Loreau 1995).

No studies have addressed the appropriate temporal and spatial scales over which stability should be evaluated or whether these scales should be the same for all ecosystems. Most studies of ecosystem processes represent periods of <5 years, although some ecosystem studies now span 40 years. The long time scales representing processes such as succession exceed the scale of human lifetimes and have required substitution of temporal variation by spatial variation (e.g., chronosequences within a landscape). Data from such studies have limited utility because individual patches have unique conditions and are influenced by the conditions of surrounding patches (Kratz *et al.* 1995, Woodwell 1993). Therefore, temporal changes at the patch scale often follow different successional trajectories.

Boulton *et al.* (1992) compared rates and directions of benthic aquatic invertebrate succession following flash floods of varying magnitude among seasons in a desert stream in Arizona, United States, over a 3-year period. Several flash floods occurred each year, but the interval between floods was long relative to the life spans of the dominant fauna. Invertebrate assemblage structure changed seasonally but was highly resistant and resilient to flooding disturbance (i.e., displacements resulting from flooding were less than were seasonal changes). By summer, robust algal mats supported dense invertebrate assemblages that were resistant to flooding disturbance. By fall, algal mat disruption made the associated invertebrate community more vulnerable to flooding disturbance. Assemblages generally returned to preflood structure, although trajectories varied widely. Long-term community structure was relatively consistent, despite unpredictable short-term changes.

Van Langevelde *et al.* (2003) proposed a model of African savanna dynamics in which alternate vegetation states cycle over time as a result of the interactive effects of fire and herbivory. Positive feedback between grass biomass and fire intensity is disrupted by grazing, which reduces fuel load, fire intensity, and tree mortality. Increased woody vegetation causes a change in state from grass dominance to tree dominance. Browers respond to increased tree abundance, reducing woody biomass and stimulating grass growth, causing the cycle to repeat. Such a system may be relatively stable over long time periods but appear unstable over short transition periods.

Although individual patches may change dramatically over time, or recover to variable endpoints, the dynamic mosaic of ecosystem types (e.g., successional stages or community types) at the landscape or watershed scale may stabilize the proportional area represented by each ecosystem type (see Chapter 10). Changing land-use practices have disrupted this conditionally stable heterogeneity of patch types at the landscape scale.

Finally, the time frame of stability must be considered within the context of the ecosystem. For example, forests appear to be less stable than grasslands because of the long time period required for recovery of forests to predisturbance conditions compared to rapid refoliation of grasses from surviving underground rhizomes. However, forests usually are disturbed less frequently. NPP may recover to predisturbance levels within 2–3 years, although biomass requires longer periods to reach predisturbance levels (e.g., Boring *et al.* 1988, Scatena *et al.* 1996, J. Zimmerman *et al.* 1996).

D. Regulation of Net Primary Productivity by Biodiversity

The extent to which biodiversity contributes to ecosystem stability has been highly controversial (see Chapter 10). Different species have been shown to control different aspects of ecosystem function (e.g., production, decomposition, and nutrient fluxes), demonstrating that biodiversity in its broadest sense affects ecosystem function (Beare *et al.* 1995, Vitousek and Hooper 1993, Waide *et al.* 1999, Woodwell 1993). The presence or absence of individual species affects biotic, atmospheric, hydrospheric, and substrate conditions (e.g., Downing and Leibold 2002). However, relatively few species have been studied sufficiently, under different conditions, to evaluate their effects on ecosystem functions. The debate depends, to a large extent, on definitions and measures of stability (see earlier in this chapter) and diversity (see Chapter 9).

Vitousek and Hooper (1993) suggested that the relationship between biodiversity and ecosystem function could take several forms. Their Type 1 relationship implies that each species has the same effect on ecosystem function. Therefore, the effect of adding species to the ecosystem is incremental, producing a line with constant slope. The Type 2 relationship represents a decreasing and eventually disappearing effect of additional species, producing a curve that approaches an asymptote. The Type 3 relationship indicates no further effect of additional species.

Communities are not random assemblages of species; instead, they are functionally linked groups of species. Therefore, the Type 2 relationship probably represents most ecosystems, with additional species contributing incrementally to ecosystem function and stability until all functional groups are represented (Vitousek and Hooper 1993). Further additions have progressively smaller effects, as species packing within functional groups simply redistributes the overall contribution among species. Hence, ecosystem function is not linearly related to diversity (Waide *et al.* 1999).

Within-group diversity could affect the persistence or sustainability of a given function, more than its rate or regulation, and thereby increase the reliability of that function (Fig. 15.2) (Naeem 1998, Naeem and Li 1997). Tilman *et al.* (1997) reported that both plant species diversity and functional diversity significantly influenced six ecosystem response variables, including primary productivity and nitrogen pools in plants and soil, when analyzed in separate univariate regressions but that only functional diversity significantly affected these variables in a multiple regression. Hooper and Vitousek (1997) also found that variability in ecosystem parameters was significantly related to the composition of functional groups, rather than the number of functional groups, further supporting the concept of complementarity among species or functional groups. Fukami *et al.* (2001) investigated the mathematical relationship between such compartmentalized biodiversity and ecosystem stability. They concluded that biodiversity loss

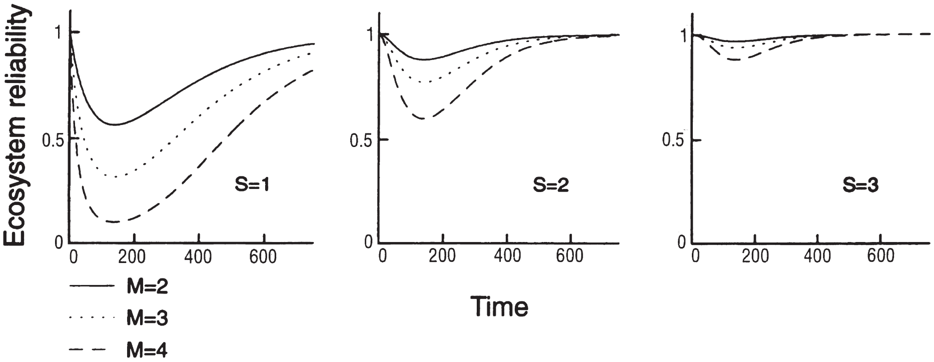


FIG. 15.2 Ecosystem reliability over time as a function of the number of functional groups (*M*) and number of species per functional group (*S*) for a probability of species colonization over time of 0.005 and a probability of species presence over time of 0.005. From Naeem (1998) with permission from Blackwell Science, Inc. Please see extended permission list pg 573.

reduces similarity in species composition among local communities and thereby reduces the reliability (stability) of continued ecosystem processes.

Dominant organisms in any ecosystem are adapted to survive environmental changes or disturbances that recur regularly with respect to generation time. Therefore, adaptation to prevailing conditions (evolution) constitutes a feedback that reduces ecosystem deviation from nominal conditions. For example, many grassland and pine forest species are adapted to survive low-intensity fires and drought (e.g., underground rhizomes and insulating bark, respectively) that characterize these ecosystems, thereby stabilizing vegetation structure and primary production. Diverse communities may be more resistant to spread of host-specific insects or pathogens (see Chapters 6 and 7). However, spread of generalists may increase with diversity, where diversity ensures a greater proportion of hosts (Ostfeld and Keesing 2000).

All ecosystems are subject to periodic catastrophic disturbances and subsequent community recovery through species replacement (succession). Ecosystem diversity at large spatial or temporal scales provides for reestablishment of key species from neighboring patches or seed banks. The rapid development of early successional communities limits loss of ecosystem assets, especially soil and limiting nutrients. Hence, succession represents a mechanism for reducing deviation in ecosystem parameters, but some early or mid successional stages are capable of inhibiting further succession. Herbivores may be instrumental in facilitating replacement of inhibitive successional stages under suitable conditions (see Chapter 10).

Few studies have measured the effect of biodiversity on stability of ecosystem parameters. Most are based on selection of plots that differ in plant species diversity and, therefore, potentially are confounded by other factors that could have produced differences in diversity among plots.

McNaughton (1985, 1993b) studied the effects of plant species diversity on the persistence and productivity of biomass in grazed grasslands in the Serengeti Plain in East Africa. Portions of areas differing in plant diversity were fenced to exclude ungulate grazers. Stability was measured as both resistance (change in productivity resulting from grazing) and resilience (recovery to fenced control condition following cessation of grazing). Grazing reduced diversity 27% in more diverse communities but had no effect on less diverse communities. The percentage biomass eaten was 67% and 76% in the more and less diverse communities, respectively, a nonsignificant difference. By 4 weeks after cessation of grazing, the more diverse communities had recovered to 89% of control productivity, but the less diverse communities recovered to only 31% of control productivity, a significant difference.

McNaughton (1977, 1993b) also compared resistance of adjacent grasslands of differing diversities to environmental fluctuation. Stability, measured as resistance to deviation in photosynthetic biomass, increased with diversity, as a result of compensation between species with rapid growth following rain but rapid drying between showers and species with slower growth after showers but slower drying between showers. Eight of 10 tests demonstrated a positive relationship between diversity and stability (McNaughton 1993b).

Frank and McNaughton (1991) similarly compared effects of drought on plant species composition among communities of differing diversities in Yellowstone National Park in the western United States. Stability of species composition to this environmental change was strongly correlated to diversity (Fig. 15.3).

Ewel (1986) and Ewel *et al.* (1991) evaluated effects of experimental manipulation of plant diversity on biogeochemical processes in a tropical rainforest in Costa Rica. This study included five treatments: a diverse natural succession, a modified succession with the same number and growth form of successional species but no species in common with natural succession, an enriched species diversity with species added to a natural succession, a crop monoculture (replicates of three different crop species), and bare ground (vegetation-free). After 5 years this design yielded plots with no plants (vegetation-free), single species (monoculture), >100 species (natural and modified succession), and 25% more species (enriched succession). Elemental pool sizes always were significantly larger in the more diverse plots, reflecting a greater variety of mechanisms for retention of nutrients and maintenance of soil processes favorable for plant production. The results suggested a Type 2 relationship between biodiversity and stability, with most change occurring at low species diversity. However, the absence of intermediate levels of diversity, between the monoculture and >100 species treatments, limited interpolation of results.

Tilman and Downing (1994) established replicated plots, in 1982, in which the number of plant species was altered through different rates of nitrogen addition. These plots subsequently (1987–1988) were subjected to a record drought. During the drought, plots with >9 species averaged about half of their predrought biomass, but plots with <5 species averaged only about 12% of their predrought biomass (Fig. 15.4). Hence, the more diverse plots were better buffered against this disturbance because they were more likely to include drought-tolerant species compared to less diverse plots. More diverse plots also recovered biomass more quickly following the drought. When biomass was measured in 1992, plots with ≥6 species had biomass equivalent to predrought levels, but plots with ≤5

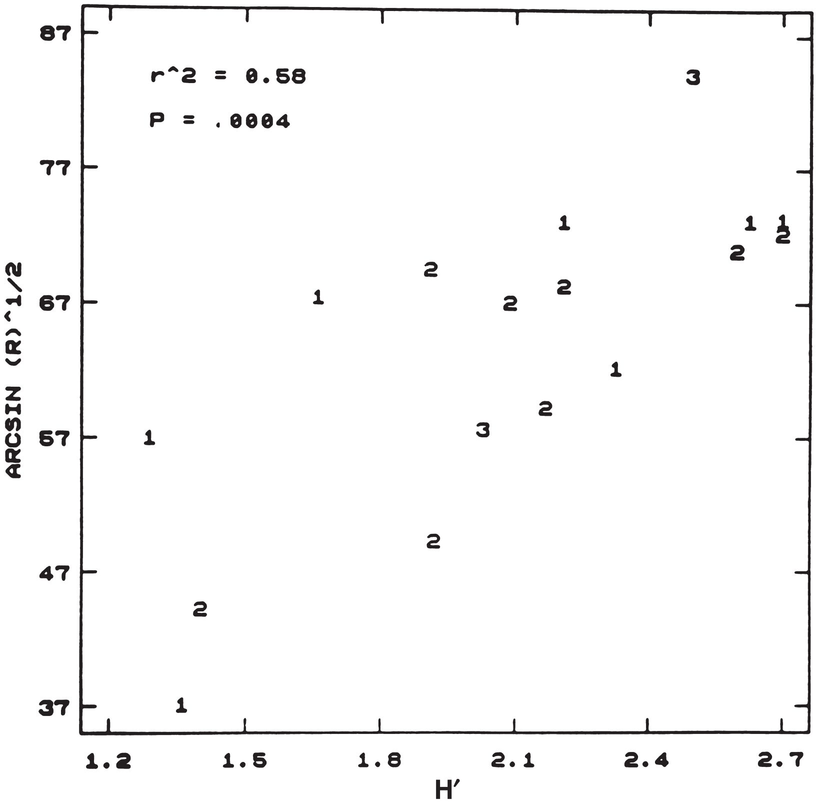


FIG. 15.3 Relationship between stability (measured as resistance [R] to change in species abundances, in degrees) and diversity (*H′*) in grasslands subject to grazing and drought at Yellowstone National Park, Wyoming. 1, early season, ungrazed; 2, peak season, grazed; 3, peak season, ungrazed. From Frank and McNaughton (1991) with permission from Oikos. Please see extended permission list pg 573.

species had significantly lower biomass, with deviations of 8–40% (Fig. 15.5). Tilman and Downing (1994) and Tilman *et al.* (1997) concluded that more diverse ecosystems represented a greater variety of ecological strategies that confer both greater resistance and greater resilience to environmental variation. However, the contribution of diversity to ecosystem stability may be related to environmental heterogeneity (i.e., diversity does not necessarily increase stability in more homogeneous environments).

A number of studies have demonstrated that ecosystem resistance to elevated herbivory is positively correlated to vegetation diversity (e.g., McNaughton 1985, Schowalter and Lowman 1999, Schowalter and Turchin 1993; see Chapters 6 and 7). As vegetation diversity increases, the ability of any particular herbivore species to find and exploit its hosts decreases, leading to increasing stability of herbivore–plant interactions.

Experimental studies relating ecosystem stability to diversity generally have been limited to manipulation of plant species diversity. However, diversity usually increases from lower to higher trophic levels. Insects represent the bulk of diversity in virtually all ecosystems (e.g., Table 9.1) and are capable of controlling a

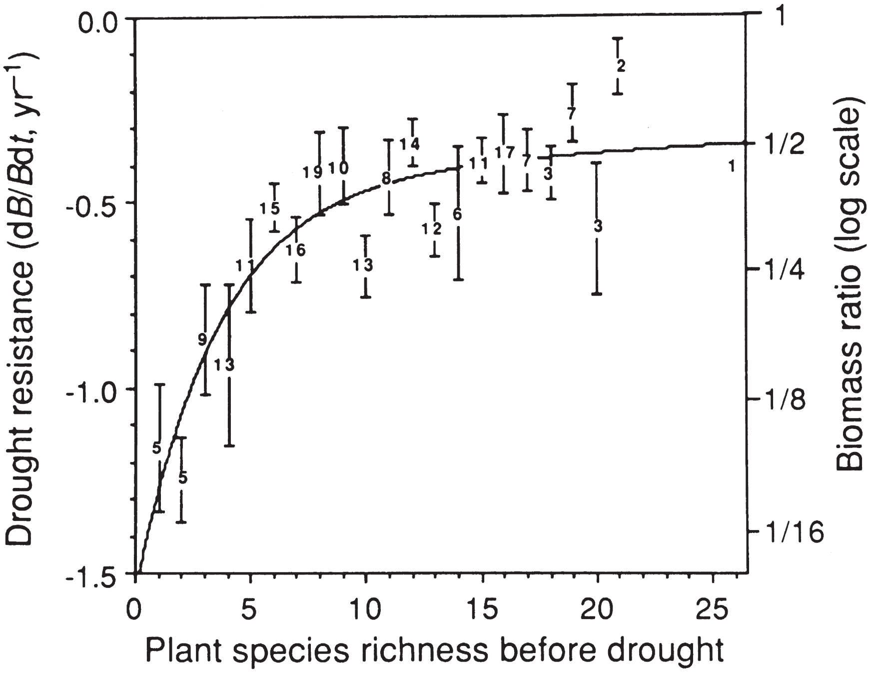


FIG. 15.4 Relationship between plant species diversity prior to drought and drought resistance in experimental grassland plots planted with different species diversities. Mean, standard error, and number of plots with given species richness are shown. 1 dB/Bdt (yr^{-1}) = 0.5 ln (1988 biomass/1986 biomass), where 1988 was the peak drought year and 1986 was the year preceding drought. The biomass 1988 : 1986 ratio (*righthand scale*) indicates the proportional decrease in plant biomass associated with dB/Bdt values. From Tilman and Downing (1994) with permission from Nature, © 1994 Macmillan Magazines, Ltd.

variety of ecosystem conditions (Chapters 12–14). A few studies have addressed the significance of diversity at higher trophic levels to ecosystem processes but not to ecosystem stability (Downing and Leibold 2002, Lewinsohn and Price 1996).

Klein (1989) found that diversity of dung beetles (Scarabaeidae) and the rate of dung decomposition were positively correlated to the size of forest fragments in central Amazonia. However, abiotic conditions that also affect decomposition likely differed among fragment sizes as well.

Coûteaux *et al.* (1991) manipulated diversity of decomposer communities in microcosms with ambient or elevated concentrations of CO_2. They found that decomposition and respiration rates were significantly related to decomposer diversity, as affected by species shifts following CO_2 treatment. This study demonstrated an effect of biodiversity on rates of a key ecosystem process but did not address long-term stability of this process.

Downing and Leibold (2002) evaluated the effects of manipulated species composition nested within multitrophic diversity treatments in pond mesocosms. The effect of species composition on productivity, respiration, and

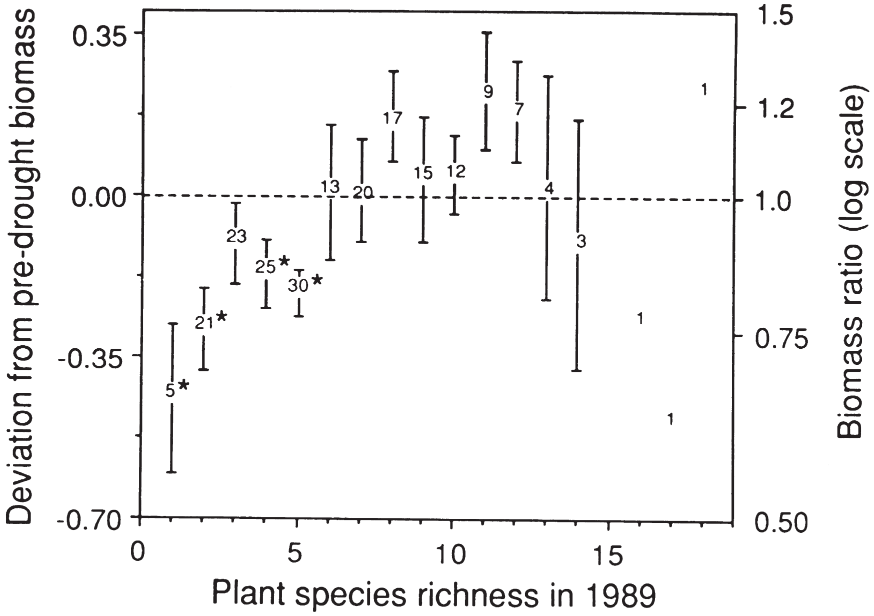


FIG. 15.5 Relationship between plant species diversity and deviation in 1992 biomass (following drought) from mean (1982–1986) predrought biomass in experimental grassland plots planted with different species diversities. Mean, standard error, and number of plots with given species richness are shown. Negative values indicate 1992 biomass lower than predrought mean. Biomass ratio is biomass 1992/predrought. Plots with 1, 2, 4, or 5 species (but not plots with >5 species) differed significantly from predrought means. From Tilman and Downing (1994) with permission from Nature, © 1994 Macmillan Magazines, Ltd.

decomposition was equivalent to, or greater than, the effect of diversity *per se.* Productivity was highest in the highest diversity treatments.

Herbivore and predator diversities have not been experimentally manipulated in terrestrial ecosystems to evaluate the effect of diversity at these levels on processes at lower trophic levels, except for biological control purposes, which may not represent interactions in natural ecosystems. For example, McEvoy *et al.* (1993) manipulated the abundances of two insect species with complementary feeding strategies (cinnabar moth, *Tyria jacobaeae,* a foliage and inflorescence feeder, and ragwort flea beetle, *Longitarsus jacobaeae,* a root feeder) introduced to control the exotic ragwort, *Senecio jacobaea,* in coastal Oregon, United States. Their results indicated that increasing diversity (from no herbivores to one herbivore to both herbivores) decreased local stability of the herbivore–plant interaction, as increasing herbivory drove the host to local extinction, at the plot scale. However, this plant species persisted at low densities over the landscape, suggesting that the interaction is stable at larger spatial scales. Croft and Slone (1997) reported that European red mite, *Panonychus ulmi,* abundances in apple orchards were maintained at lower, equilibrial, levels by three predaceous mite species than by any single predaceous species.

Ultimately, the capacity of ecosystems to endure or modify the range of environmental conditions is the primary measure of stability (McNaughton 1993b) (see Fig. 15.2). In this regard, Boucot (1990) noted that the fossil record demonstrates that characteristic species assemblages (hence, ecosystems) often have persisted for many thousands of years over large areas.

E. Regulation of Net Primary Productivity by Insects

During the 1960s, a number of studies, including Crossley and Howden (1961), Crossley and Witkamp (1964), C. Edwards and Heath (1963), and Zlotin and Khodashova (1980), indicated that arthropods potentially control energy and nutrient fluxes in ecosystems. Clearly, phytophages could affect, without regulating, ecosystem properties. However, phytophages respond to changes in vegetation density or physiological condition in ways that provide both positive and negative feedback, depending on the direction of deviation in primary production from nominal levels (Figs. 12.5 and 15.6).

Mattson and Addy (1975) introduced the hypothesis that phytophagous insects regulate primary production, based on observations that low intensities of herbivory on healthy plants often stimulate primary production, but high intensities of herbivory on stressed or dense plants suppress primary production.

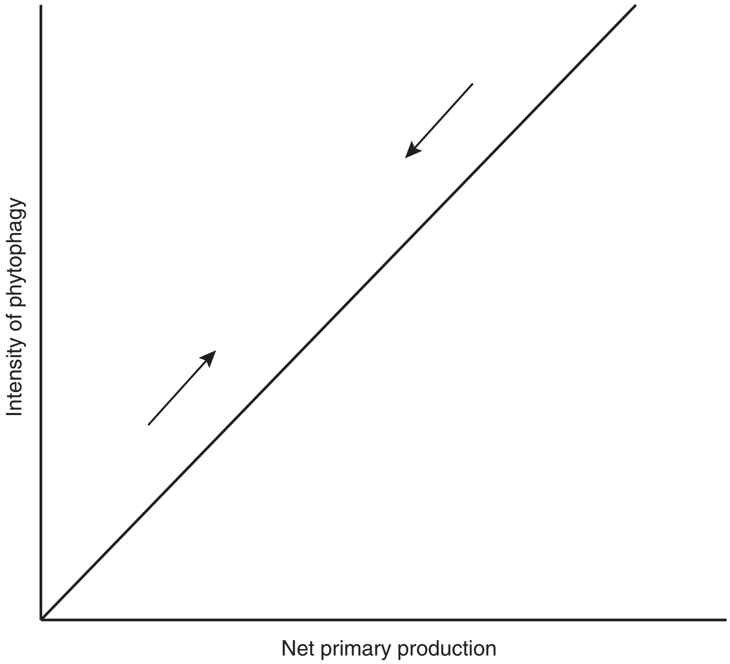


FIG. 15.6 Stimulation of primary production at net primary productivity (NPP) < K and suppression of primary production at NPP > K by phytophages (see Fig. 12.5) could stabilize primary production. From Schowalter (2000) with permission from CABI.

Furthermore, productivity by surviving plants often is greater following herbivore outbreaks (see Chapter 12). Schowalter (1981) proposed that phytophage outbreaks, triggered by host stress and density as resources become limiting, function to advance succession from communities with high demands for resources to communities with lower demands for resources. Davidson (1993) and Schowalter and Lowman (1999) refined this hypothesis by noting that herbivores and granivores can advance, retard, or reverse succession, depending on environmental conditions. Belovsky and Slade (2000) demonstrated that grasshoppers can accelerate nitrogen cycling and increase primary productivity, especially by plants that are better competitors when nitrogen is more available, at intermediate levels of herbivory. At low levels of herbivory, grasshoppers had too little influence on nitrogen cycling to affect primary production. At high levels, grasshoppers depressed plant growth and survival more than could be offset by increased nitrogen cycling and plant productivity.

Despite the obvious influence of animals on key ecosystem processes, their regulatory role has remained controversial and largely untested. Herbivorous insects possess the characteristics of cybernetic regulators (i.e., low maintenance cost and rapidly amplified effects, sensitivity to deviation in ecosystem parameters, and capacity to dramatically alter primary production through positive and negative feedback) and appear, in many cases, to stabilize NPP. For example, inconsequential biomass of phytophagous insects, even at outbreak densities, is capable of removing virtually all foliage from host plants and altering plant species composition (see Chapter 12). Virtually undetectable biomass of termites accounts for substantial decomposition, soil redistribution, and gas fluxes that could affect global climate (see Chapter 14). The following model for insect effect on ecosystem stability focuses on herbivores, but detritivores, pollinators, and seed dispersers also are capable of modifying ecosystem conditions in ways that might promote stability (e.g., decomposer enhancement of nutrient availability, plant growth, and herbivory [Holdo and McDowell 2004] provides feedback on herbivore effects on litter quality and availability [S. Chapman *et al.* 2003]).

Primary production often peaks at low to moderate intensities of pruning and thinning (see Fig. 12.5), supporting the grazing optimization hypothesis (Belovsky and Slade 2000, S. Williamson *et al.* 1989). Herbivores apparently stimulate primary production at low levels of herbivory, when host density is low or condition good, and reduce primary production at high levels, when host density is high or condition is poor (Fig. 15.6), potentially stabilizing primary production at intermediate levels. Furthermore, primary production often is higher following herbivore outbreaks than during the preoutbreak period (e.g., Alfaro and Shepherd 1991, Romme *et al.* 1986), suggesting alleviation of stressful conditions that could lead to instability. By stabilizing primary production, herbivores also stabilize internal climate and soil conditions, biogeochemical fluxes, etc., that affect survival and reproduction of associated organisms. Romme *et al.* (1986) reported that mountain pine beetle, *Dendroctonus ponderosae,* outbreaks appeared to increase variation (destabilization) of some ecosystem properties. However, these outbreaks represent a response to an anthropogenic deviation in primary production (i.e., increased tree density resulting from fire suppression).

No data are available to indicate whether long-term variation in ecosystem parameters is reduced by such outbreaks. However, annual wood production following mountain pine beetle outbreaks equaled or exceeded preoutbreak levels within 10 years, suggesting relatively rapid recovery of primary production (Romme *et al.* 1986).

Outbreaks of phytophagous insects are most likely to occur under two interrelated conditions, both of which represent responses to departure from nominal ecosystem conditions, often resulting from anthropogenic alteration (Schowalter 1985, Schowalter and Lowman 1999). First, adverse environmental conditions, such as inadequate water or nutrient availability, changing climate, and atmospheric pollution, cause changes in plant physiological conditions that increase suitability for phytophages. High intensities of herbivory under these conditions generally reduce biomass and improve water or nutrient balance or, in extreme cases, reduce biomass of the most stressed plants, regardless of their abundance, and promote replacement by better adapted plants (e.g., Ritchie *et al.* 1998, Schowalter and Lowman 1999). Second, high densities of particular plant species, as a result of artificial planting or of inhibitive successional stages, enhance host availability for associated phytophages. High intensities of herbivory represent a major mechanism for reversing site dominance by such plant species, facilitating their replacement and increasing diversity.

If communities evolve to minimize environmental variation, then herbivore interactions with disturbances are particularly important. Although outbreaks of herbivores traditionally have been viewed as disturbances (together with events such as fire, storm damage, and drought), their response to host density or stress often appear to reduce the severity of abiotic disturbances. Herbivore outbreaks commonly co-occur with drought conditions (Mattson and Haack 1987, T. White 1969, 1976, 1984), suggesting that plant moisture stress may be a particularly important trigger for feedback responses that reduce transpiration and improve water balance (W. Webb 1978). Fuel accumulation, as a result of herbivore-induced fluxes of material from living to dead biomass, often predisposes ecosystems to fire in arid environments. Whether such predisposition is stabilizing or destabilizing depends on the degree to which outbreaks modify the severity and temporal or spatial scale of such disturbances. Schowalter (1985) and Schowalter *et al.* (1981a) suggested that herbivore-induced disturbances might occur more regularly with respect to host generation times or stages of ecosystem development, as a result of specific plant–herbivore interactions, and thereby facilitate rapid adaptation to disturbance or postdisturbance conditions. Although such induction of disturbance would seem to increase variation in the short term, accelerated adaptation would contribute to stability over longer time periods. Furthermore, increased likelihood of disturbance during particular seres should maintain that sere on the landscape, contributing to stability over larger spatial scales. The following example demonstrates the potential stabilization of ecosystem properties over the large spatial scales of western North America.

Conifer forests dominate much of the montane and high latitude region of western North America. The large, contiguous, lower elevation zone is characterized by relatively arid conditions and frequent droughts that historically maintained a sparse woodland dominated by drought- and fire-tolerant (but shade-intolerant) pine trees and a ground cover of grasses and shrubs, with little understory (Fig. 15.7). Low-intensity ground fires occurred frequently, at intervals of 15–25 years, and covered large areas (Agee 1993), minimizing drought-intolerant vegetation and litter accumulation. The relatively isolated higher elevation and riparian zones were more mesic and supported shade-tolerant (but fire- and drought-intolerant) fir and spruce forests. Fire was less frequent (every 150–1000 years) but more catastrophic at higher elevation as a result of the greater tree densities and understory development that facilitated fire access to tree canopies (Agee 1993, Veblen *et al.* 1994).

As a result of fire suppression during the past century, much of the lower elevation zone has undergone succession from pine forest to later successional fir

FIG. 15.7 The relatively arid interior forest region of North America was characterized by open-canopied forests dominated by drought- and fire-tolerant pines, and by sparse understories, prior to fire suppression beginning in the late 1800s (**A**). Fire suppression has transformed forests into dense, multistoried ecosystems stressed by competition for water and nutrients (**B**). From Goyer *et al.* (1998) with permission from the Society of American Foresters.

FIG. 15.7 (*Continued*)

forest (see Fig. 15.7), a conspicuous deviation from historic conditions. Outbreaks of a variety of folivore and bark beetle species have become more frequent in these altered forests. During mesic periods and in more mesic locations (e.g., riparian corridors and higher elevations) the mountain pine beetle has advanced succession by facilitating the replacement of competitively stressed pines by more competitive firs. However, during inevitable drought periods, such as occurred during the 1980s, moisture limitation increases the vulnerability of these firs to several folivores and bark beetles specific to fir species (Fig. 15.8). Insect-induced mortality of the firs reversed succession by favoring the remaining drought- and fire-tolerant pines. Tree mortality can increase the severity and scale of catastrophic fires, which historically were rare in these forests, unless litter decomposition reduces fuel accumulation before fire occurs. However, this altered fire regimen likely will be mitigated in ecological time by eventual reestablishment of the pine sere following catastrophic fire. A similar situation has been inferred from insect demography in pine-hardwood forests of the southern United States (see Fig. 10.5). Van Langevelde *et al.* (2003) also suggested a cycle of alternating vegetation states maintained by interaction of fire and herbivores in African savanna.

FIG. 15.8 Phytophage modification of succession in central Sierran mixed conifer ecosystems during 1998. Understory white fir (*Abies concolor*), the late successional dominant, is increasingly stressed by competition for water in this arid forest type. An outbreak of the Douglas-fir tussock moth, *Orgyia pseudotsugata,* has completely defoliated the white fir (*brown trees*), restoring the ecosystem to the more stable condition dominated by earlier successional, drought- and fire-tolerant sequoias and pines (*green, foliated, trees*). Photo by J. H. Jones.

To what extent do insects contribute to stability and "health" of various ecosystems? Until recently, insect outbreaks and disturbances have been viewed as destructive forces. The increased productivity of ecosystems in the absence of fire and insect outbreaks supported a view that resource production could be freed from limitations imposed by these regulators. However, fire now is recognized as an important tool for restoring sustainable (stable) ecosystem conditions and characteristic communities. Accumulating evidence also suggests that outbreaks of native insects represent feedback that maintains ecosystem production within sustainable ranges. Regulation of primary production by phytophagous insects could stabilize other ecosystem variables as well. Clearly, experimental studies should address the long-term effects of phytophagous insects on variability of ecosystem parameters. Our management of ecosystem resources, and in particular our approach to managing phytophagous insects, requires that we understand the extent to which phytophages contribute to ecosystem stability.

III. SUMMARY

The hypothesis that phytophagous insects regulate ecosystem processes is one of the most important and controversial concepts to emerge from research on insect ecology. The extent to which ecosystems are random assemblages of species that simply affect ecosystem processes or are tightly co-evolved groups of species that stabilize ecosystem function has important implications for management of ecosystem resources and "pests." Although this hypothesis is not contingent on natural selection at the supraorganismal level, concepts of group selection have developed from and contributed to this hypothesis.

Debate on the issue of group selection has solidified consensus on the dominance of direct selection for individual attributes. However, individual attributes affect other organisms and environmental conditions and generate feedback on individual fitness. Such feedback selection contributes to the inclusive fitness of an individual. The intensity of this feedback is proportional to the relatedness of interacting individuals. The greatest feedback selection is between near kin (kin selection). The frequency of interaction and the intensity of feedback selection declines as interacting individuals become less related. However, frequent interspecific interaction can lead to negative feedback (e.g., competition and predation) and reciprocal cooperation (mutualism), based on the tradeoff between gain or loss to each individual from such interaction.

Homeostasis at supraorganismal levels depends only in part on selection for attributes that benefit assemblages of organisms (i.e., group selection). The critical issue is the tradeoff required to balance individual sacrifice, if any, and inclusive fitness accruing from traits that benefit the group. Stabilization of environmental conditions through species interactions favor survival and reproduction of the constituent individuals. Therefore, feedback selection over evolutionary time scales should select for species interactions that contribute to ecosystem stability and mutually assured survival.

Major challenges for ecologists include defining stability (i.e., which ecosystem properties are stabilized, what range of deviation is tolerated, and what temporal and spatial scales are appropriate levels for measurement of stability) and evaluating the effect of mechanisms, such as biodiversity and herbivory, that contribute to stability. Traditionally, stability has been viewed as constancy or recovery of species composition over narrow ranges of time and space. Alternative views include reliability of NPP and biomass structure, which affect the stability of internal climate and soil conditions, and biogeochemical pools and fluxes over larger ranges of time and space. Stability may be achieved, not at the patch scale, but at the landscape scale where conditional stability is achieved through relatively constant proportions of various ecosystem types.

The relationship of stability to diversity has been a major topic of debate. Some species are known to control ecosystem properties, and their loss or gain can severely affect ecosystem structure or function. Furthermore, effects of different species often are complementary, such that diverse assemblages should be better buffered against changes in ecosystem properties in heterogenous environments. A few experimental manipulations of plant species diversity have shown that more diverse communities can have lower variability in primary production than do less diverse communities.

Phytophagous insects have been identified as potentially important regulators of primary production, hence of ecosystem properties determined by primary production. Phytophagous insects possess the key criteria of cybernetic regulators (i.e., small biomass, rapid amplification of effect at the ecosystem level, sensitivity to airborne or waterborne cues indicating ecosystem conditions, and stabilizing feedback on primary production and other processes). Low intensity of herbivory, under conditions of low densities or optimal condition of hosts, tends to stimulate primary production, whereas higher intensities, under conditions of high density or stressed condition of hosts, tend to reduce primary production. Clearly, this aspect of insect ecology has significant implications for our approaches to managing ecosystem resources and "pests."

SECTION V

SYNTHESIS

THE PREVIOUS FOUR SECTIONS HAVE ADDRESSED insect ecology at the individual, population, community, and ecosystem levels of organization. Resource acquisition and allocation by individuals (Section I) can be seen to depend on population (Section II), community (Section III), and ecosystem (Section IV) conditions that the individual also influences. Insects are involved in a particularly rich variety of feedbacks between individual, population, community, and ecosystem levels as a consequence of their dominance and diversity in terrestrial and freshwater ecosystems and their sensitivity and dramatic responses to environmental changes. The hypothesis that insects are major regulatory mechanisms in homeostatic ecosystems has important ecological and management implications and warrants critical testing.

The importance of temporal and spatial scales is evident at each level of the ecological hierarchy. Individuals have a period and range of occurrence, populations are characterized by temporal dynamics and dispersion patterns, and communities and ecosystems are represented over temporal and spatial scales. In particular, ecosystem stability and its effect on component individuals traditionally has been evaluated at relatively small scales, in time and space, but larger scales are more appropriate. The dynamic mosaic of ecosystem types at the landscape or biome level is conditionally stable in its proportional representation of ecosystem types.

This concluding chapter summarizes and synthesizes the study of insect ecology. The focus will be on important aspects of insect ecology, major applications, and intriguing questions for future study.

16

Synthesis

THE STUDY OF INSECT ECOLOGY TRADITIONALLY ADDRESSED INSECT adaptations to their environment, including interactions with other organisms, and effects on plant growth and vegetation structure. Insects represent the full scope of heterotrophic strategies, from sessile species whose ecological strategies resemble those of plants to social insects whose range of behavioral attributes is more like that of advanced vertebrates. The variety of insect interactions with other species spans the range of ecological complexity and often brings them to the attention of natural resource managers as pests, biological control agents, or key pollinators or seed dispersers of endangered plants. Three of the four sections in this book emphasize this traditional approach to the study of insect ecology.

However, this traditional focus on species adaptations and community interactions does not portray the full scope of insect ecology. Whereas the evolutionary perspective emphasizes insect responses to environmental conditions, as demonstrated by adaptive physiology, behavior, and interspecific interactions, the ecosystem perspective emphasizes feedbacks between organisms and their environment. Insects, as well as other organisms, influence their environment in complex, and often dramatic, ways. The foraging pattern of any organism affects its interactions with other organisms and the resulting distribution of resources. Population outbreaks of some herbivorous insects can reshape vegetation structure and alter biogeochemical cycles and local or regional climate. Natural selection represents a major feedback between ecosystem conditions and individual attributes that affect ecosystem parameters. Other feedback mechanisms between individuals, populations, and communities can stabilize or destabilize ecosystem, landscape, and global processes. Understanding these feedbacks is critical to prediction of ecosystem responses to environmental changes. Phytophages dramatically alter the structure of landscapes and potentially stabilize primary production and other processes affecting global climate and biogeochemistry (Chapter 12). Termites account for substantial portions of carbon flux in some ecosystems (Chapter 14). Section IV, dealing with feedbacks between insects and ecosystem properties, is the unique contribution of this book. This chapter summarizes key ecological issues, synthesizes key integrating variables, describes applications, and identifies critical issues for future study.

I. SUMMARY

The hierarchical organization (see Fig. 1.2 or Table 1.1) of this text emphasizes linkages and feedbacks among levels of ecological organization. Linkages and feedbacks are strongest between neighboring levels but are significant even between individual and ecosystem levels of the hierarchy. Physiological and behavioral responses to environmental variation are under genetic control and determine individual fitness, but they also affect the rate and geographic pattern of resource acquisition and allocation that control climate and energy and biogeochemical fluxes at the ecosystem level. These feedbacks are an important and largely neglected aspect of insect ecology that affect ecosystem stability and global processes.

The geographic distribution of individual species generally reflects the environmental template established by continental history, latitude, mountain ranges, and global atmospheric and oceanic circulation patterns. The great diversity of insects reflects their rapid adaptation, conferred by small size, short life spans, and rapid reproductive rates, to environmental variation. These attributes have facilitated speciation at multiple scales: among geographic regions, habitats, and resources and at microscales on or within resources (e.g., individual leaves). However, within the potential geographic range of a species, the spatial and temporal patterns of abundance reflect disturbance dynamics, resource distribution, and interactions with other species that affect individual fitnesses and enhance or limit colonization and population growth.

Energy and resource budgets (see Fig. 4.1) are key aspects of individual fitness, population persistence, and community interactions. All organisms require energy to accumulate resources, necessary for growth and reproduction, against resource concentration gradients and thereby maintain the thermodynamic disequilibrium characteristic of life. Where resources are more concentrated, relative to individual needs, less energy is required for acquisition. Interactions among organisms often may be controlled by mass balances of multiple nutrients. Resource use requires adaptations to acquire necessary limiting nutrients, such as nitrogen, while avoiding or circumventing toxic or defensive chemicals as well as overabundant nutrients.

Much research has addressed plant defenses against feeding by insects and other herbivores. Insect herbivores have evolved a variety of mechanisms for avoiding, detoxifying, or inhibiting expression of plant defenses. All species have mobile stages adapted to find new resources before current resources are depleted or destroyed. The early evolution of flight among insects greatly facilitated foraging, escape from unsuitable environmental or resource conditions, and discovery of more optimal conditions. Individuals or populations that fail to acquire sufficient energy and nutrients to grow and reproduce do not survive.

Adaptations for detecting and acquiring resources are highly developed among insects. Many insects can detect the presence and location of resources from chemical cues carried at low concentrations on wind or water currents. The diversity of strategies among insect species for acquiring resources has perhaps drawn the most ecological attention. These strategies range from ambush to active foraging; often demonstrate considerable learning ability (especially among social insects); and involve insects in all types of interactions with other organisms, including competition (e.g., for food, shelter, and oviposition site resources), predation and parasitism (on plant, invertebrate, and vertebrate prey or hosts and as prey or hosts), and mutualism (e.g., for protection, pollination, and seed dispersal).

Spatial and temporal variation in population and community structure reflects net effects of environmental conditions. Changes in population and community structure also constrain survival and reproduction of associated species. Population density and competitive, predatory, and mutualistic interactions affect foraging behavior and energy and nutrient balances of individuals. Individuals forced to move constantly to avoid intraspecific or interspecific competitors or predators will be unable to forage sufficiently for energy and nutrient resources. However, energy and nutrient balances can be improved through mutualistic interactions that enhance the efficiency of resource acquisition. The relative contributions of intraspecific and interspecific interactions to individual survival and reproduction remain a central theme of ecology but have been poorly integrated with ecosystem conditions. Debate over the importance of bottom-up versus top-down controls of populations perhaps reflects variation in the contributions of these factors among species as well as spatial and temporal variation in their effect.

Ecosystems represent the level at which complex feedbacks among abiotic and biotic processes are integrated. Ecosystems can be viewed as dynamic energy- and nutrient-processing engines that modify global energy and nutrient fluxes. Cycling and storage processes controlled by organisms reduce variation in abiotic conditions and resource availability. Although ecosystem properties are largely determined by vegetation structure and composition, insects and other animals modify ecosystem conditions, often dramatically, through effects on primary production, decomposition and mineralization, and pedogenesis. Insect herbivore effects on vegetation structure affect albedo, evapotranspiration, and wind abatement. Changes in decomposition processes affect fluxes of carbon and trace gases as well as soil structure and fertility. Insect roles as ecosystem engineers mitigate or exacerbate environmental changes resulting from anthropogenic activities. Resolution of environmental issues requires attention to these roles of insects as well as to their responses to environmental changes.

II. SYNTHESIS

Insect ecology addresses an astounding variety of interactions between insects and their environment. However, key aspects of insect ecology involve feedback between insect responses to changes in environmental conditions, especially resource supply, and their capacity to modify, and potentially stabilize, energy and nutrient fluxes. As shown throughout this text, each level of hierarchical organization can be described in terms of characteristic structure, function, and feedback regulation. Feedback integration among hierarchical levels occurs primarily through responses to, and modification of, variation in environmental conditions (see Fig. 1.2). Insect behavioral and physiological attributes that affect their interactions with the environment are under genetic control. Evolution represents feedback on individual attributes that affect higher levels of organization.

The importance of environmental change and disturbance as a central theme in insect ecology has been recognized only recently. Disturbance, in particular, provides a context for understanding and predicting individual adaptations, population strategies, organization and succession of community types, and rates and regulation of ecosystem processes. Environmental changes or disturbances kill individuals or affect their activity and reproduction. Some populations are reduced to local extinction, but others exploit the altered conditions. Population strategies and interactions with other species also affect ecosystem properties in ways that increase the probability of disturbance (or other changes) or that mitigate environmental changes and favor persistence of species less tolerant to change. Insects contribute greatly to feedback between ecosystem properties and environmental variation. This aspect of insect ecology has important consequences for ecosystem responses to global changes resulting from anthropogenic activities.

Energy and biogeochemical fluxes integrate individuals, populations, and communities with their abiotic environment. Energy flow and biogeochemical cycling processes determine rates and spatial patterns of resource availability. Many, perhaps most, species attributes can be shown to represent tradeoffs between maximizing resource acquisition and optimizing resource allocation among metabolic pathways (e.g., foraging activity, defensive strategies, growth, and reproduction). The patterns of energy and nutrient acquisition and allocation by individuals determine the patterns of storage and fluxes among populations; fluxes among species at the community level; and storage and flux at the ecosystem level that, in turn, determine resource availability for individuals, populations, and communities. Resource availability is fundamental to ecosystem productivity and diversity. Resource limitation, including reduced availability resulting from inhibition of water and nutrient fluxes, is a key factor affecting species interactions. Herbivore and predator populations grow when increasing numbers of hosts or prey are available or incapable of escape or defense because of insufficient resource acquisition or poor food quality.

Regulatory mechanisms emerge at all levels of the ecological hierarchy. Negative feedback and reciprocal cooperation are apparent at population, community, and ecosystem levels. Cooperation benefits individuals by improving ability to acquire limiting resources. This positive feedback balances the negative feedbacks that limit population density, growth, and ecological processes. At the population level, positive and negative feedbacks maintain density within narrower ranges than occur when populations are released from regulatory mechanisms. The responsiveness of insect herbivores to changes in plant density and condition, especially resulting from crop management, introduction into new habitats, and land use, bring some species into conflict with human interests. However, insect outbreaks in natural ecosystems appear to be restricted in time and space and function to (1) maintain net primary production (NPP) within relatively narrow ranges imposed by the carrying capacity of the ecosystem and (2) facilitate replacement of plant species that are poorly adapted to current conditions by species that are better adapted to these conditions. Regulatory capacity appears to reflect selection for recognition of cues that signal changes in host density or condition that affect long-term carrying capacity of the ecosystem.

The issue of ecosystem self-regulation is a key concept that significantly broadens the scope of insect ecology. Although this idea remains controversial, accumulating evidence supports a view that insect outbreaks function to reduce long-term deviation in NPP, at least in some ecosystems. Although outbreaks appear to increase short-term variation in some ecosystem parameters, reversal of unsustainable increases in NPP could reduce long-term variation in ecosystem conditions.

Models of group selection predict that stabilizing interactions are most likely in ecosystems where pairs of organisms interact consistently. Hence, selection for stabilizing interactions might be least likely in ecosystems where such interactions are inconsistent, such as in harsh or frequently disturbed environments. However, selection for stabilizing interactions also might be less direct in productive, highly diverse ecosystems with little variation in abiotic conditions or resource availability, such as tropical rainforest ecosystems. Stabilizing interactions are most likely in ecosystems where selection would favor interactions that reduce moderate levels of variation in abiotic conditions or resource availability.

Insects play key roles in regulation of primary and secondary production. Their large numbers, rapid reproduction, and mobility may maximize their interactions with other organisms and the rate at which they evolve reciprocal cooperation.

III. APPLICATIONS

Insect ecology represents the intersection between basic understanding of how insects interact with their environment and necessary applications for pest management, ecosystem restoration, and other aspects of ecosystem management. Understanding feedbacks between insects and their environment provides useful information for understanding insects in the broader context of ecosystem and global processes. Although insect outbreaks occur in natural ecosystems when conditions are favorable, anthropogenic changes in ecosystem conditions often promote population growth of species that are viewed as "pests." These changes often can be reversed or mitigated with adequate ecological information. Insect ecology also addresses the variety of insect effects on ecosystem conditions. Such information is necessary to determine when suppression of outbreaks may be warranted to meet specific management goals.

A. Management of Crop, Forest, and Urban "Pests"

Management of crop, forest, and urban "pests" has been a major application of insect ecology. Insect roles in ecosystems may conflict with crop and livestock production and human health and habitation when conditions favor insect population growth. For example, densely planted monocultures of crop species, often bred to reduce bitter (defensive) flavors, provide ideal conditions for population growth of herbivorous species (see Chapter 6). Similarly, buildings provide protected habitats for ants, termites, cockroaches, and other species, especially when moisture and unsealed food create ideal conditions. Insects become viewed as pests when their activities conflict with human values.

Traditional views of herbivorous and detritivorous insects as destructive, or at least nuisances, and ecological communities as nonintegrated, random assemblages of species supported harsh control measures. Early approaches to insect control included arsenicals, although much classic research on population regulation by predators and parasites also occurred prior to World War II. With the advent of broad-spectrum, long-lived, chlorinated hydrocarbons and organophosphates, developed as nerve toxins and used for control of disease vectors in combat zones during World War II, management of insects seemed assured. However, reliance on these insecticides exposed many target species to intense selection over successive generations and led to rapid development of resistant populations of many species (Soderlund and Bloomquist 1990). Concurrently, movement of the toxins through food webs resulted in adverse environmental consequences that became widely known in the 1960s through publication of Rachel Carson's *Silent Spring* (1962).

The last legal use of DDT (dichlorodiphenyltrichloroethane) in the United States, against the Douglas-fir tussock moth, *Orgyia pseudotsugata,* in 1974 during an outbreak in Oregon and Washington required emergency authorization by the U.S. Environmental Protection Agency, which had canceled use of DDT in the United States in 1972 (Brookes *et al.* 1978). This emergency authorization, based on apparent lack of practical alternatives, mandated intensified research on alternative methods of control. Although the importance of nuclear polyhedrosis virus, *Baculovirus* spp., in terminating tussock moth outbreaks had been known since the 1960s, applications of DDT or other chemicals reduced larval densities to levels incapable of supporting epizootics (Brookes *et al.* 1978) and masked the importance of natural regulatory mechanisms. Subsequent research has demonstrated that enhancement of epizootics by application of technical-grade viral preparation to first instar larvae can cause population collapse within the same year; this currently is the preferred means of control. Accumulating evidence indicates that the Douglas-fir tussock moth may be an important regulator of forest conditions (see Chapter 15): compensatory timber production following outbreaks offsets economic losses (Alfaro and Shepherd 1991, Wickman 1980).

Much subsequent research has addressed the effects of pesticide residues on nontarget organisms and has led to cancellation of registration for chemicals with adverse environmental effects and to development and use of more specific chemicals, including insect growth regulators (IGRs) and chitin sythesis inhibitors (CSIs), with shorter half-lives in the environment. Research results also have led to greater use of microbial pathogens, including nuclear polyhedrosis viruses (NPV) and *Bacillus thuringiensis* (Bt). Effectiveness of these tools can be enhanced by attention to ecological factors. For example, invasive ants and termites, which often are inaccessible to broadcast application of toxins, can be controlled effectively by attracting foragers to a bait containing nonrepellent, slow-acting toxin, IGR, or CSI that is shared with nestmates through trophyllaxis, accomplishing population reduction with minimal effect on nontarget species.

Much ecological research also has demonstrated the importance of using multiple tactics, including elimination of conducive conditions, enhanced plant defenses, insect growth regulators, pheromones, predators, and parasites, that constitute an integrated pest management (IPM) approach (e.g., Barbosa 1998, Huffaker and Messenger 1976, Kogan 1998, Lowrance *et al.* 1984, Rabb *et al.* 1984, Reay-Jones *et al.* 2003, Rickson and Rickson 1998, Risch 1980, 1981). An ecological approach emphasizes multiple tactics representing the combination of bottom-up, top-down, and lateral factors that regulate natural populations. For example, increased tree spacing can interrupt bark beetle and defoliator outbreaks in forests, reducing the likelihood of outbreaks and need for pesticides. Agroforestry and multiple-cropping systems that increase crop diversity also can interrupt spread of insect populations (Fig. 16.1). In addition, elicitors of induced defenses, such as jasmonic acid, could be used to elevate resistance to pests in crop plants and stimulate biological control at appropriate times (M. Stout *et al.* 2002). Because of the delay in expression of induced defenses, this approach would be most effective when infestations can be reliably anticipated and economic thresholds are high. Augmentation or introduction of predator and parasite populations for biological control requires retention of necessary habitat, such as native vegetation in hedgerows, or alternative resources, such as floral nectar sources (Hassell *et al.* 1992, Landis *et al.* 2000, Marino and Landis 1996, Thies and Tscharntke 1999). Implementation of control measures should be based on predictive models that indicate when the insect population is expected to exceed a calculated threshold, based on net cost–benefit of insect effect and control, above which intolerable loss of economic or environmental values would occur if the population is not controlled (Rabb *et al.* 1984).

Herbivorous insects also have been used to control invasive plant species. Introducing biological control agents from the pest's region of origin requires consideration of their ability to become established in the new community and their effects on nontarget species, as well as on the costs and benefits of invasive plant persistence and insect introduction.

Many crop species have been genetically engineered to express novel defenses, such as Bt toxins. However, reliance on such strategies threatens to undermine their long-term effectiveness, given insect ability to evolve resistance. Therefore, a high-dose-with-refuge strategy is recommended to prevent survival of pests on the Bt crop and maintain a large, nonadapted population in non-Bt refuges (Alstad and Andow 1995, Carriére *et al.* 2003). Management of resistance

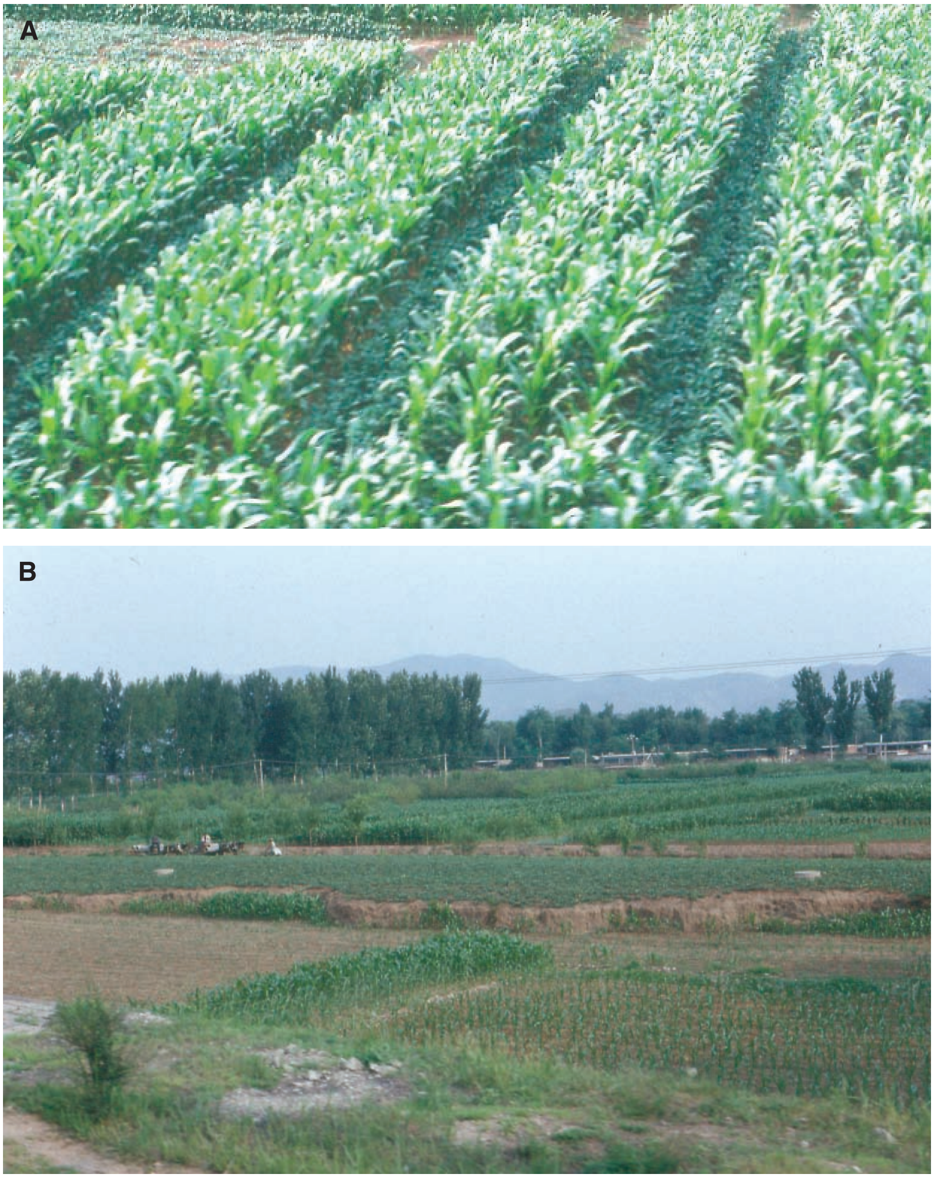


FIG. 16.1 Examples of multiple cropping to hinder spread of insect species over agricultural landscape in northeastern China. **A:** Embedded intercropping within rows. **B:** Multiple crop species arranged in strips.

development to transgenic crops could be undermined if pollen contamination of nontransgenic refuges or native vegetation leads to variable Bt concentrations and effects on nontarget species in the landscape (Chilcutt and Tabashnik 2004, Zangerl *et al.* 2001). This requires attention to the landscape structure of Bt and non-Bt crops (especially for insects with broad host ranges that might include multiple transgenic crops) and cooperation among scientists, growers, and government agencies (Carrière *et al.* 2001a). Another promising new tool includes use of chemicals, such as jasmonic acid, to elicit expression of targeted defenses by crop plants (e.g., M. Stout *et al.* 2002, Thaler 1999b, Thaler *et al.* 2001). However, expression of defenses by plants depends on adequate resources.

Advances in understanding of insect effects on a variety of plant and ecosystem attributes also has influenced evaluation of the need for insect management. Furthermore, management goals for natural ecosystems has become more complex in many regions, as societal needs have changed from a focus on extractive uses (e.g., fiber, timber, or livestock production) to include protection of water yield and quality, fisheries, recreational values, biodiversity, and ecosystem integrity. In many cases, insect outbreaks now are viewed as contributing to, rather than detracting from, management goals for natural or seminatural ecosystems. Recognition that low levels of herbivory stimulate primary production by many plants, including crop species (Pedigo *et al.* 1986, Trumble *et al.* 1993, S. Williamson *et al.* 1989), and may affect soil structure, infiltration, fertility, and climate requires evaluation of the integrated effects, or net cost–benefit, of changes in insect abundance or activity.

Many serious human diseases, such as malaria, yellow fever, bubonic plague, and equine encephalitis, are vectored by arthropods among humans and other animal species, especially rodents and livestock. Rodents are reservoirs for several important human diseases, but horses and cattle also are sources of inoculum. West Nile virus has a particularly broad reservoir of hosts, including birds, small mammals, and reptiles. The rapid spread of this disease across North America between 1999 and 2004 reflected a combination of insect transmission of the virus among multiple hosts and rapid bird movement across the continent (Marra *et al.* 2004). The importance of these diseases to human population dynamics, including the success of military campaigns, underscores the importance of understanding human roles in ecological interactions. Increasing human intrusion into previously unoccupied ecosystems has exposed humans to novel animal diseases that may involve insect vectors. Transmission frequency increases with density of human, reservoir, or vector populations. Management must involve a combination of approaches that augment natural controls and reduce exotic breeding habitat for vectors (e.g., tires, flower pots, roadside ditches) or reservoir hosts as well as inoculation of humans who may be exposed.

Termites, carpenter ants, and wood-boring beetles often threaten wooden structures. Considerable investment has been made in research to reduce damage, especially in historically important buildings. Again, management requires multiple approaches, including chemical barriers to make buildings less attractive to these insects; removal or treatment of infested building material, nearby wood waste, or infested trees; pheromone disruption of foraging behavior; nonrepellent termiticides that can be transferred in lethal doses to other colony members through trophyllaxis; and microbial toxins to inhibit gut flora and fauna (J. K. Grace and Su 2001, Shelton and Grace 2003). Other urban "pests" include nuisances and health hazards, such as exotic ants, biting or swarming flies, and even winter aggregations of ladybird beetles, that may be promoted by proximity of lawns, gardens, and ornamental pools. Frequent pesticide application or elimination of native vegetation in urban settings often reduces the abundance of desirable insects, such as butterflies, dragonflies, and biological control agents. Understanding the ecological factors that promote or suppress these insects in urban settings will enhance management strategies.

B. Conservation/Restoration Ecology

Relatively few studies have addressed insects as part of ecosystem conservation or restoration projects. Some endangered insects, such as the Fender's blue butterfly, *Icaricia icarioides fenderi,* and American burying beetle, *Necrophorus americanus,* are targets for conservation or restoration efforts (M. Wilson *et al.* 1997). However, insects also can affect the success of conservation or restoration projects focused on other species or integrated communities.

Loss of key species or functional groups would jeopardize ecosystem integrity and lead to degradation. Xylophages may be particularly threatened as a result of deforestation, forest fragmentation, and conversion of landscapes dominated by old forests with abundant woody litter to landscapes dominated by young forests with little woody litter accumulation. Numerous wood-boring species became extinct as a result of deforestation of Europe during the past 5000 years (Grove 2002). Loss of specialized pollinators or seed dispersers as a result of habitat fragmentation also would threaten the survival of plant mutualists (Powell and Powell 1987, Somanathan *et al.* 2004, Steffan-Dewenter and Tscharntke 1999). Ants and ground beetles (Carabidae) are important predators in many ecosystems but are sensitive to changes in ecosystem condition, potentially undermining their role as predators (A. Andersen and Majer 2004, Niemelä and Spence 1994, Niemelä *et al.* 1992). Such groups should be identified for inclusion in conservation or restoration efforts.

Restoration goals need to address the appropriate historic conditions. For example, clearcut harvest and replanting of ponderosa pine, *Pinus ponderosa,* or Douglas-fir, *Pseudotsuga menziesii,* in western North America reflected the early perception of fire as a stand replacing disturbance that burned the forest and created a mineral soil seed bed necessary for establishment of even-aged forest. The resulting even-aged monocultures have supported nearly continuous insect outbreaks as the forests age. More recent research following natural fires in the region demonstrated more complex effects of fire, with patches of surviving trees intermingled with patches burned to mineral soil, resulting in uneven-aged forest structure as forest expanded from the refuges. Consequently, restoration efforts currently focus on thinning and prescribed fire to produce uneven-aged forest structure, and wider tree spacing, often aided by insects (J. Stone *et al.* 1999). At the same time, restoration of these forests to uneven aged, more widely spaced trees, maintained by a restored low-intensity fire regimen, should improve tree physiological condition and reduce the likelihood of future insect outbreaks (Kolb *et al.* 1998).

Restoration also requires attention to critical site conditions. Planted seedlings may be insufficient for forest restoration on harsh sites. Amaranthus and Perry (1987) demonstrated that transfer of biologically active soil (containing invertebrates and microorganisms necessary for maintenance of soil fertility) from established conifer plantations significantly increased the survival and growth of seedlings on clearcut harvested sites by up to 50% compared to seedlings planted directly into clearcut soils from which soil biota had disappeared as a result of overstory removal and exposure to heat and desiccation. Similarly, flooding a depression may not be sufficient for wetland restoration. Attention to water flux and predisposing substrate conditions may be necessary for reestablishment of wetland vegetation. For example, S. C. Brown *et al.* (1997) found that transplantation of wetland soil resulted in significantly faster and more prolific plant growth and macroinvertebrate colonization. Insects often serve as useful indicators of ecosystem conditions and restoration success (A. Andersen and Majer 2004).

Second, restoration of some ecosystems requires attention to insect mutualists necessary for reproduction and survival of target species. Research on the ecology of pollination and seed dispersal has demonstrated the critical role insects play in the persistence of understory and sparsely distributed plant species (Chapter 13). If necessary pollinators or seed dispersers disappear in isolated refuges (e.g., Fig. 13.3), other means must be found to ensure reproduction and recruitment of target plant species. For example, evaluation and promotion of alternate pollinators or seed dispersers may be necessary, recognizing that such species may be less efficient than those that co-evolved with a particular plant species.

Finally, restoration success can be threatened by invasive species. Invasive plants can outcompete target plants, requiring consideration of insect herbivores as biological control agents. Invasive insects also can create problems. For example, red imported fire ants, *Solenopsis invicta,* negatively affect populations of ground-nesting birds, small mammals, and reptiles and can discourage larger animals from entering infested areas (C. Allen *et al.* 2004). Introduced diseases, such as insect-vectored plague and West Nile virus, can decimate wildlife populations (Marra *et al.* 2004, Stapp *et al.* 2004), requiring consideration of tactics to reduce vector or pathogen abundance to ensure successful conservation or restoration of vulnerable species. At the same time, invasive species are not necessarily detrimental to restoration efforts and may, in some cases, contribute to restoration success (Ewel and Putz 2004).

C. Indicators of Environmental Conditions

As we increase our understanding of insect responses to environmental factors, insects become useful indicators of changing conditions (Dufrêne and Legendre 1997). Because of their sensitivity to climate or biochemical changes in their resources and rapid reproductive rates, insects may provide early warning of changes not yet apparent in the condition or abundance of plants or vertebrates, usually favored as bioindicators.

Insects have proved to be useful indicators of changing water quality (Hawkins *et al.* 2000). Chironomid midges have proved to be particularly useful indicators of water quality in aquatic ecosystems. For example, replacement of chironomid species characterizing oligomesotrophic conditions by species characterizing eutrophic conditions provided early indication of pollution in Lake Balaton, Hungary (Dévai and Moldován 1983, Ponyi *et al.* 1983).

Ant associations are used as indicators of ecosystem integrity and the status of restoration efforts in Australia (A. Andersen and Majer 2004). Similarly, grasshopper (see Fig. 5.7), dung beetle (see Fig. 9.6), and ground beetle assemblages can be used to assess ecosystem integrity and recovery status (Fielding and Brusven 1995, Klein 1989, Niemelä and Spence 1994, Niemelä *et al.* 1992). Because of their sensitivity to host defenses, insect herbivores could be used as indicators of change in plant biochemistry before visible chlorosis or other symptoms of stress become apparent.

The sequence of insect species occurrence during heterotrophic succession in decomposing carcasses has been applied by law enforcement agencies. Heterotrophic succession in carrion (see Figs. 10.3 and 10.4) provides the foundation for determining time of death under various environmental conditions (Byrd and Castner 2001, Goff 2000, K. Smith 1986, E. Watson and Carlton 2003). For example, the rate of fly colonization of a corpse differs between exposed or protected locations. Research on the sequence and timing of colonization by various insect species on corpses under different environmental conditions has contributed to establishing time of death and opportunity by suspected perpetrators. This has enhanced the ability of law enforcement officials to convict murderers and wildlife poachers.

D. Ecosystem Engineering

Insects have the capacity to alter environmental conditions dramatically. In addition to changing vegetation structure, they alter the rate and direction of energy and material flows through ecosystems and landscapes. In some cases, this may be a useful tool for accomplishing management objectives in natural ecosystems. Fire increasingly is recognized as an integral component of many ecosystems and is being used, or allowed to burn freely, to maintain ecosystem conditions. Although still controversial, insect outbreaks under some circumstances could be viewed as contributing to the maintenance or restoration of ecosystem conditions (Figs. 15.6–15.8), including stimulation of nutrient fluxes, and might be allowed to run their course. This action would require the cooperation of various land management agencies responsible for the affected, and surrounding, landscape.

IV. CRITICAL ISSUES

Resolution of the debate concerning potential regulatory roles of insects in natural ecosystems may not be possible, given the need for large-scale manipulation of insect populations and long-term, multidisciplinary comparison of ecosystem processes necessary to test the hypothesis. However, more data are needed on long-term consequences of insect activities in relatively natural ecosystems, including effects of population changes on mass balances of energy and nutrient fluxes, because these may mitigate or exacerbate effects of acid rain, carbon flux, and other processes affecting global change. Our perspective on the role of insects determines our management approaches. Whether we view insects as disturbances that destabilize ecosystems or as regulators that contribute to stability determines not only our approach to managing insects in natural or engineered ecosystems but also our approaches to managing our ecosystem resources and responding to global changes.

Clearly, exotic species freed from both bottom-up and top-down regulation function in the same way as pollutants or exotic disturbances (i.e., with little ecosystem control over their effects), at least initially. By contrast, population size and effects of native species are regulated by a variety of bottom-up, top-down, and lateral factors. Adaptations of native species to disturbances shape responses to natural or anthropogenic alteration of vegetation and landscape structure, with effects that often are contrary to management goals but perhaps conducive to ecological balances. If native insects function as regulators that contribute to ecosystem stability, then traditional management approaches that emphasize suppression may interfere with this natural feedback mechanism and maintain anthropogenic imbalances, at least in some ecosystems. In any case, insect outbreaks usually are responses to high density or stress of host plants, or both, making outbreaks a form of feedback that stabilizes ecosystem conditions, rather than a pest problem. Long-term solutions, therefore, require remedies for the departure from stability, rather than simply suppression of outbreaks.

Predicting and alleviating effects of anthropogenic changes requires understanding of insect roles and how these roles affect ecosystem responses to anthropogenic changes. Anthropogenic changes will continue to trigger insect outbreaks, whether as destructive events or regulatory responses. Land use, in particular, affects patch structure and interactions among demes, greatly altering the spatial and temporal patterns of insect abundances. Ruderal plant species, valued for crop production but also adapted for rapid colonization of new habitats, are increasingly likely to dominate fragmented landscapes. The rapid growth and poor competitive ability of these species in crowded ecosystems make them targets for their associated insects. Such ecosystems will require constant human intervention. Protection or restoration of natural ecosystems will require attention to interactions necessary to maintain key species, including pollinators, seed dispersers, and decomposers.

Accomplishment of this primary goal requires broadening of research approaches to address the breadth of insect effects on ecosystem structure and function. This, in turn, requires changes in research approaches and integration of population and ecosystem models. Testing of ecosystem-level hypotheses involves different approaches than does testing of population- and community-level hypotheses. At least three considerations are particularly important.

First, experimental design requires attention to statistical independence of samples. Whereas individuals within populations can serve as replicates for population and community properties, data must be pooled at the site (ecosystem) level for comparison of ecosystem variables. Ecosystem studies often have provided inconclusive data because a single site representing each of several ecosystem types or experimental treatments (e.g., Fig. 16.2 B-1 and B-2) provides

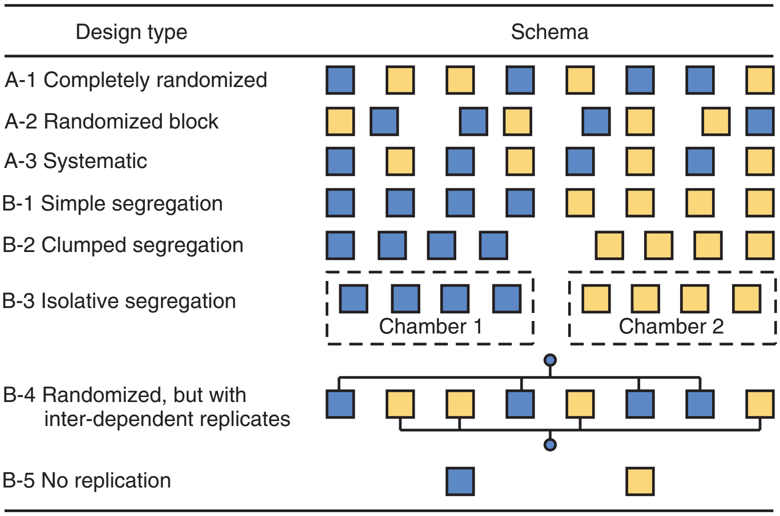


FIG. 16.2 Three representations (*A-1–A-3*) of acceptable experimental designs with interspersed, independent replicates of two treatments (*shaded vs. unshaded boxes*) and five representations (*B-1–B-5*) of experimental designs in which the principle of interspersed, independent replicates can be violated. From Hurlbert (1984) with permission from the Ecological Society of America. Please see extended permission list pg 573.

no error degrees of freedom for statistical analysis. Multiple samples collected within each site are not statistically independent (Hurlbert 1984). Furthermore, treatment effects are subject to confounding effects of geographic gradients between treatment plots. Therefore, experimental designs must incorporate multiple, geographically interspersed, replicate sites representing each ecosystem type or treatment (Fig. 16.2 A-1–A-3). A larger number of replicate sites provides a greater range of inference than do multiple samples within sites (that must be pooled for statistical analysis), requiring a tradeoff in sampling effort within sites and between sites.

Second, research to evaluate insect responses to, or effects on, ecosystem conditions should address a greater range of ecosystem variables than has been common in past studies of insect ecology. Insects respond to multiple factors simultaneously, not just one or a few factors subject to experimental manipulation, and their responses reflect tradeoffs that might not be reflected in studies that control only one or a few of these factors. A greater breadth of parameters can be addressed through multidisciplinary research, with experts on different aspects of ecosystems contributing to a common goal (Fig. 16.3). Involvement of insect ecologists in established multidisciplinary projects, such as the International Long Term Ecological Research (ILTER) sites in many countries, can facilitate integration of insect ecology and ecosystem ecology. Specifically, insect ecologists can contribute to such programs by clarifying how particular species respond to, and shape, ecosystem conditions, including vegetation structure, soil properties, biogeochemical cycling processes, etc., as described in Chapters 12–14; how insects affect the balance of nutrient fluxes within and between

FIG. 16.3 Interdisciplinary research on insect effects on log decomposition at the H. J. Andrews Experimental Forest Long Term Ecological Research Site in western Oregon, United States. **A:** Logs tented to exclude wood-boring insects during the first year of decomposition. **B:** Logs inoculated with different initial heterotroph communities (bark vs. wood-borer, mold vs. decay fungi; ribbon color indicates inoculation treatment; plastic shelters reduced wood moisture relative to unsheltered logs). Data loggers at each replicate site measured ambient temperature and relative humidity and vertical and horizontal temperature and moisture profiles in logs. Sticky screens were used to measure insect colonization, emergence traps were used to measure insect emigration, PVC (polyvinyl chloride) chambers were used to measure CO_2 flux, and funnels under logs were used to measure water and nutrient flux out of logs. Scheduled destructive sampling of logs provided data on changes in wood density, excavation by insects, and nutrient content.

ecosystems (e.g., from aquatic to terrestrial ecosystems or across landscapes as populations move or expand, as described in Chapter 7); and how species diversity within guilds or functional groups affects the reliability of community organization and processes (Chapter 15).

Third, spatial and temporal scales of research and perspectives must be broadened. Most ecosystem studies address processes at relatively small spatial and temporal scales. However, population dynamics and capacity to influence ecosystem and global properties span landscape and watershed scales, at least. Feedbacks often may be delayed or operate over long time periods, especially in ecosystems with substantial buffering capacity, requiring long-term institutional and financial commitments for adequate study. Linkage of population and ecosystem variables using remote sensing and GIS (geographic information system) techniques will become an increasingly important aspect of insect ecology. Nevertheless, ecosystems with large biomass or high complexity require simplified field mesocosms or modeling approaches to test some hypotheses.

The complexity of ecosystem interactions and information linkages has limited incorporation of detail, such as population dynamics, in ecosystem models. Modeling methodology for ecosystem description and prediction is necessarily simplified, relative to that for population models. However, population models have largely ignored feedbacks between population and ecosystem processes. Hierarchical structure in ecosystem models facilitates integration of more detailed insect population (and other) submodels, and their linkages and feedbacks with other levels, as data become available (see Fig. 11.15).

Several ecosystem components should be given special attention. Subterranean and forest canopy subsystems represent two ecological frontiers. Logistical difficulties in gaining nondestructive or nonintrusive access to these two subsystems have limited data available for insect effects on canopy-atmosphere and canopy–rhizosphere–soil interactions that control climate and energy and matter fluxes. Improved canopy access methods, such as construction cranes (Fig. 16.4) for ecological use (Schowalter and Ganio 1998, D. Shaw 1998, 2004), and rhizotron technology (Sackville Hamilton *et al.* 1991, Sword 1998) offer opportunities for scientific advances in the structure and function of these subsystems.

Finally, principles of insect ecology must be applied to improved management of insect populations and ecosystem resources. Ecosystem engineering can make crop systems more or less conducive to insect population irruptions. Alternative cropping systems include protection of soil systems to enhance energy and matter availability and polyculture cropping and landscape patterns of crop patches and remnant native vegetation (see Fig. 16.1) to restrict herbivore dispersal among hosts or patches (Coleman *et al.* 1992, Kogan 1998, Lowrance *et al.* 1984, Rickson and Rickson 1998, Risch 1980, 1981). These cropping systems also enhance conditions for predators that control potentially irruptive insect species. Promotion of interactions that tend to stabilize populations of irruptive species is more effective in the long term than is reliance on pesticides or genetically engineered crops. Examples include provision or retention of hedgerows, ant-attracting plants, or

FIG. 16.4 Canopy cranes are a new tool for experimental access to forest canopies. For example, the gondola of the Wind River Canopy Crane (75-m tall tower, 84-m long jib) can access 700,000 m^3 of 60-m tall canopy, as well as the canopy-atmosphere interface, over a 2.3-ha area in a 500-year-old *Pseudotsuga/Tsuga* forest in southwestern Washington, United States. Photo by J. F. Franklin, from D. Shaw (2004). Please see extended permission list pg 573.

other refuges within agricultural landscapes that maintain predator populations (Kruess and Tscharntke 1994, Rickson and Rickson 1998). Furthermore, insect effects on ecosystems, including agroecosystems, are complex. Net effects of outbreaks on multiple parameters should be considered in deciding whether to suppress outbreaks. Given that outbreaks often reflect simplification of ecosystem conditions and function to restore complexity and, perhaps, stability, control of native species in natural ecosystems may be counterproductive. Letting outbreaks run their course could serve management purposes under some conditions.

IV. CONCLUSIONS

Insects are involved in virtually all aspects of terrestrial and freshwater ecosystems. Environmental issues directly or indirectly involve insects, either in their capacity to respond to environmental changes or their capacity to alter ecosystem conditions. Therefore, insect ecology is fundamental to our ability to understand ecosystem structure and function and to solve environmental problems.

The hierarchical ecosystem approach to insect ecology emphasizes linkages and feedbacks among individual, population, community, and ecosystem levels and clarifies the basis and consequences of insect adaptive strategies. This approach also indicates which level best addresses environmental problems. For example, if the issue is factors controlling plant susceptibility to herbivores, then individual responses to environmental cues are the appropriate focus. If the issue is spread of exotic species or restoration of native species, then metapopulation dynamics and regulatory interactions within communities are the levels of focus. If the issue is factors affecting global mass balances of carbon fluxes, then mass balances at the ecosystem level are the appropriate focus.

Our most significant scientific advances in the next decades will be in demonstrating the degree to which ecosystems modify environmental conditions and persist in the face of changing global conditions. Insects are major contributors to the ways in which ecosystems modify local and global conditions. Natural selection can be viewed as a major form of feedback between ecosystem conditions and individual adaptations that modify or stabilize ecosystem parameters. The degree to which insects regulate ecosystem parameters remains a key issue and one that significantly broadens the scope and value of insect ecology.

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