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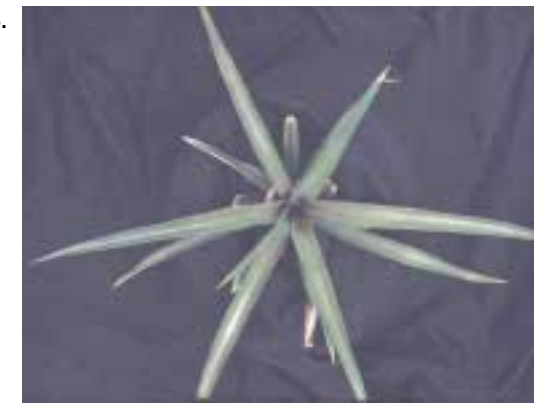

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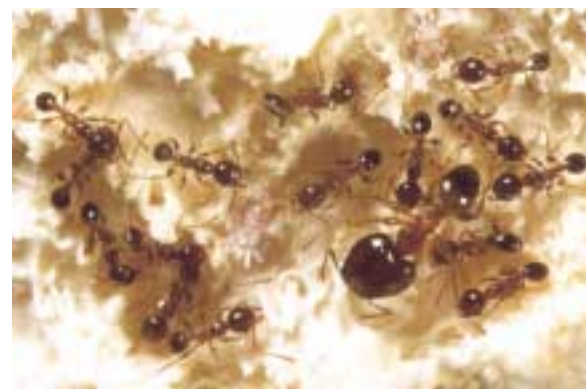

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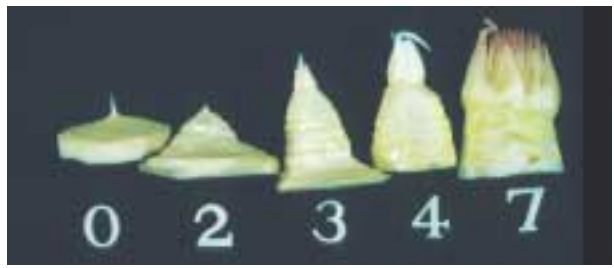

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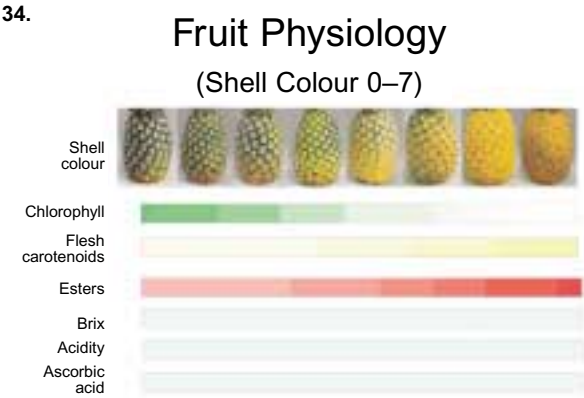

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The Pineapple

Botany, Production and Uses

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Edited by

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Preface

Pineapple is the third most important tropical fruit in world production after banana and citrus. Seventy per cent of the pineapple produced in the world is consumed as fresh fruit in the country of origin. This worldwide production has developed since the early 1500s when pineapple was first taken to Europe and then distributed throughout the world's tropics. International trade is dominated by a few multinational companies that have developed the infrastructure to process and market pineapple. The most famous variety in world trade is Cayenne Lisse ('Smooth Cayenne'), which was introduced to Europe from French Guiana. Many clones of this cultivar are known and a number of other cultivars are only grown regionally for consumption in the country of production or represent a minor component of the fresh-fruit export market.

Drought tolerance and the ease of transport of vegetative propagules facilitated the wide diffusion of pineapples around the world. However, the relatively short shelf-life of fresh pineapple fruit limited early commercial trade to relatively short transportation routes or a preserved form of the fruit. The commercial processing of pineapple started in Hawaii at the end of the 19th century and Hawaii was a world leader in pineapple research and processing until after the Second World War. The invention and refinement of the automatic peeling and coring machine by Henry Ginaca in Hawaii, between 1911 and 1919, allowed the development of a large-scale economically viable canning industry. This was paralleled by the major expansion of pineapple production and expanded research on the crop.

This book is the outcome of discussions between the editors over the past 10 years. The most recent comprehensive book on pineapple was published in French in 1983 and an English version with minor additions was published in 1987. That book is now out of print. The need for such a book was also seen as opportune, as many of the individuals involved in the research associated with the international expansion of pineapple production and marketing were retiring. This book is an attempt to put in one place a synopsis of the worldwide research findings and commercial practices, mainly for 'Smooth Cayenne', but mention is made of other cultivars where they differ from 'Smooth Cayenne' and where published information was available.

The book integrates genetics, breeding, physiology, pathology, handling and processing

with commercial practices. Successful commercial production requires not only an integration of these findings, but their management in different biotic and abiotic environments and with different market needs. The information contained in the book should be of use to all interested in pineapple production and utilization.

Many have contributed to this text. The editors wish to thank the individual chapter authors for their patience and understanding. Special thanks are due to Valent BioSciences Corporation, California, for a generous donation that allowed us to include the eight pages of colour plates. Tania Ishimaru worked for many hours typing and editing and checking the individual chapters, and her help is sincerely appreciated by the editors. All errors and omissions are the responsibility of the editors.

In closing, we would like to dedicate this book to the many scientists who spent much of their life working on pineapple. Cristos Sideris, Walter Carter, J.L. Collins, Claude Py and Eloys Giacommelli warrant special mention for their many contributions to the advancement of pineapple science and culture. Many scientists at the Pineapple Research Institute of Hawaii contributed much to our knowledge of pineapple, but their work was done for private growers and so remains largely unpublished. We hope progress will continue to be made in understanding this unique and fascinating crop.

Duane Bartholomew
Kenneth Rohrbach
Robert E. Paull
Honolulu, 2002

1 History, Distribution and World Production

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Early History

Prior to the discovery of the pineapple fruit by Cristobal Colón (Christopher Columbus) on 4 November 1493 (Morrison, 1963), the fruit was already a stable component of the vegetative-crop complex and in the diet of native Americans in the lowland tropics (Laufer, 1929). The European explorers were impressed by this large and delicious fruit and often mentioned and described it in their chronicles. These early reports indicate that domesticated pineapple was already very widely distributed in the Americas (Orinoco, Amazon, coastal Brazil around Rio de Janeiro) and the Caribbean prior to the arrival of Columbus (Collins, 1960). In some cases, the Europeans themselves could have contributed to pineapple dispersion in the continent. Indeed, the many plants (e.g. lemon, orange, sugar cane, banana and plantain) introduced by Colón from the Canary Islands since his second voyage were distributed by the natives throughout tropical America in less than two decades, as evidenced by banana and plantain cultivation in Puerto Bello in 1503 (Colón, 1506). On the other hand, if the natives dispersed these new crops so quickly, they very probably had done the same with pineapple long before Colón. Other evidence points to the antiquity of pineapple cultivation. Thus, the names 'nanas' and 'ananas' were extensively used throughout South America and the Caribbean. Early European explorers observed a high degree of domestication and selection exhibited in the pineapples they found. The Amerindians easily distinguished landraces from the wild types and had developed a thorough knowledge of the crop agronomy, including its production cycle. Specifically adapted landraces (e.g. the Andean 'Perolera' and 'Manzana') were found with variation in fruit yield and quality. Five additional centuries of work by talented horticulturists and modern plant breeders have not added significantly to the variety of domesticated types (Leal and Coppens d'Eeckenbrugge, 1996; Coppens d'Eeckenbrugge *et al*., 1997).

In addition to the fresh fruit, the native Americans used pineapple for the preparation of alcoholic beverages (pineapple wine, *chicha* and *guarapo*), for the production of fibre, and for medicinal purposes, as an emmenagogue, abortifacient, antiamoebic and vermifuge and for the correction of stomachal disorders, and for the poisoning

 The Pineapple: Botany, Production and Uses (eds D.P. Bartholomew, R.E. Paull and K.G. Rohrbach)

of arrowheads. Most of these medicinal uses are related to the proteolytic enzyme bromelain of the pineapple (Leal and Coppens d'Eeckenbrugge, 1996). The native Americans also domesticated the *curagua*, a smooth-leaved type with a higher yield of long and strong fibres, and used it for making nautical and fishing-lines, fishing nets, hammocks and loincloths (Leal and Amaya, 1991). There is still a small traditional industry based on pineapple fibre in Brazil (Leme and Marigo, 1993) and even in the Philippines, where 'piña cloth' was mentioned as early as 1571 (Collins, 1960; Montinola, 1991).

From the early 1500s, the pineapple fascinated the Europeans, who introduced and grew it in greenhouses. The first successful greenhouse cultivation was by Le Cour, or La Court, at the end of the 17th century near Leyden. He published a treatise on pineapple horticulture, including 'forcing' the plants to flower. Pineapple plants were distributed from The Netherlands to English gardeners in 1719 and to France in 1730 (Gibault, 1912). As pineapple cultivation in European greenhouses expanded during the 18th and 19th centuries, many varieties were imported, mostly from the Antilles. Griffin (1806) described ten of them and considered most of the others as useless and their cultivation cumbersome. Others have described numerous varieties (Loudon, 1822; Munro, 1835; Beer, 1857). The now famous variety Cayenne Lisse ('Smooth Cayenne') was introduced from French Guiana by Perrotet in 1819 (Perrotet, 1825). With the notable exceptions of 'Smooth Cayenne' and 'Queen', most of these early varieties disappeared as commercial cultivation in Europe declined and pineapple fruit was imported from the West Indies.

'Smooth Cayenne' and 'Queen' were taken from Europe to all tropical and subtropical regions (Fig. 1.1; Collins, 1951). The Spaniards and Portuguese dispersed other varieties, including 'Singapore Spanish', to Africa and Asia during the great voyages of the 16th and 17th centuries. However, the diversity of these varieties is still negligible compared with the variation found in America. 'Smooth Cayenne' is by far the most important variety in world trade; many others are only grown regionally for local consumption. Both Smooth Cayenne and Singapore Spanish can be called true cultivars (see Coppens d'Eeckenbrugge and Leal, Chapter 2, this volume).

Development of the Pineapple Trade

Drought tolerance and the ease of transport of vegetative propagules facilitated the wide diffusion of pineapples around the world. However, the relatively short shelf-life of fresh pineapple fruit limited early commercial trade to relatively short transportation routes or some form of preservation. Jams and sweets made in the West Indies, Brazil and New Spain (Mexico) were the first commercial products of pineapple (Thévet, 1557; Acosta, 1590; Loudon, 1822). In the early 19th century, fresh pineapples were sent from the West Indies to Europe attached to the entire plant, which lowered the price in the European markets and led to a decline in European glasshouse production (Loudon, 1822). Commercialization during the mid-19th century developed based on the shortest trade routes rather than an optimum pineapple production environment. Production in Florida, the Bahamas, Cuba and Puerto Rico supplied the North American market and the Azores the European market. The Azores maintained their monopoly of the European fresh-fruit market until after the Second World War, when production shifted to Africa (Py *et al.*, 1987).

Commercial processing of pineapple started in Hawaii at the end of the 19th century. The invention and refinement of the automatic peeling and coring machine by Henry Ginaca, a Hawaiian Pineapple Company (Dole) employee, between 1911 and 1919 allowed the development of a large-scale economically viable canning industry. This was paralleled by a major expansion of pineapple production. The 1919 *ginaca* peeled and cored up to 65 pineapples min^{-1}. A 1925 model, also developed by the Hawaiian Pineapple Company, processed 90–100 pineapples min^{-1}. No additional sig-

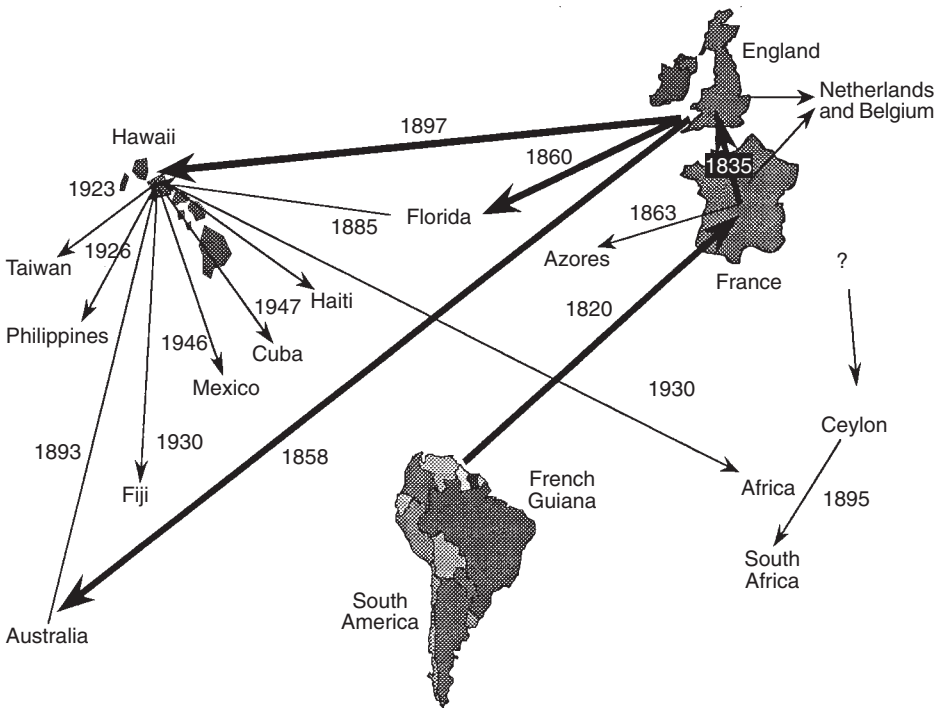

Fig. 1.1. Distribution of the 'Smooth Cayenne' cultivar (after Collins, 1951).

nificant improvements have been made on this machine since 1925 (Anon., 1993). Other important canning operations started around the same period in South-East Asia (Malaysia in 1888, Taiwan in 1902, Philippines in 1920), Australia, South Africa, the Caribbean (Martinique, Cuba and Puerto Rico) and Kenya. The Second World War ruined the South-East Asian industry and destroyed international trade. Hawaii gained a strong leadership position that lasted until the development of new competitors (Côte d'Ivoire and the Philippines, followed by Thailand) between 1950 and the early 1960s. In these same years, refrigerated sea transportation developed and diminished the importance of proximity to the market. Hawaii, West Africa (mainly Côte d'Ivoire) and Taiwan shifted part of their production to the fresh-fruit market, exporting, respectively, to the North American, European and Japanese markets. Philippine production expanded greatly in the 1970s, exporting canned products and significant quantities of fresh fruit to Japan (Py *et al*., 1987). Today, the canned-product market remains very important but the value of the international fresh-fruit market is rapidly increasing.

World Production and Trade

Pineapple is now the third most important tropical fruit in world production after banana and citrus. The processing of pineapple has made the fruit well known throughout the temperate developed world. Major pineapple products of international trade are canned slices, chunks, crush (solid pack) and juice and fresh fruit (Fig. 1.2). International trade is dominated by a few multinational companies that have developed the infrastructure to process and market pineapple. Thailand and Indonesia are, to a degree, exceptions, with small local processing operations. Despite the significance of canned pineapple in international trade, approximately 70% of the pineapple produced in the

world is consumed as fresh fruit in the country of origin (Loeillet, 1997). Important producing countries, such as Brazil, India, China, Nigeria, Mexico and Colombia, produce fruit primarily for their own fresh-fruit markets and canning is a minor industry.

Statistics on world pineapple production are collected by the Food and Agriculture Organization of the United Nations (FAO). According to FAO statistics (Baker, 1990; Anon., 2002), total pineapple production was approximately constant in the 1999–2001 period, with a mean world production for these 3 years of 13,527,149 metric tonnes (t). World production has more than tripled during the past 30 years (3,833,137 t in 1961 to 13,738,735 t in 2001). The leading pineapple-producing countries are Thailand with 2,311,332 t, the Philippines with 1,520,715 t and Brazil with 1,504,493 t (means 1999–2001). China (1,181,169 t), India (1.1 million t), and, Nigeria (800,000 t) follow. Nigerian statistics announced year after year are a surprisingly constant 800,000 t. Other producers exceeding 250,000 t are Mexico (535,000 t), Costa Rica (475,000 t), Colombia (360,000 t), Indonesia (300,000 t), Venezuela (300,000 t), USA (293,000 t) and Kenya (280,000 t). The value of these statistics is relative to their accuracy. Thus, the joint use of statistics for production and planted areas allows yield estimations ranging from a high (and unlikely) of 48 t ha^{-1} for Cuba to a low of 7 t ha^{-1} for Indonesia (Table 1.1). Indeed, several countries are thought to give rough estimates, which may explain the surprising official production of countries such as Nigeria and the low correlation between yields and the probable level of technology and inputs used in the production system. In addition, FAO statistics do not separate fresh fruit from processed pineapple or export from local consumption.

Pineapple produced in Thailand and the Philippines dominates world trade. The former country processes approximately 1.6 million t of its total production of 2 million t. Thailand's pineapple is produced on almost 100,000 ha of small farms of 1–5 ha (Anupunt *et al.*, 2000). In contrast to Thailand, production and marketing in the Philippines is almost exclusively run by multinational corporations using large plantation production systems. Export and marketing from the

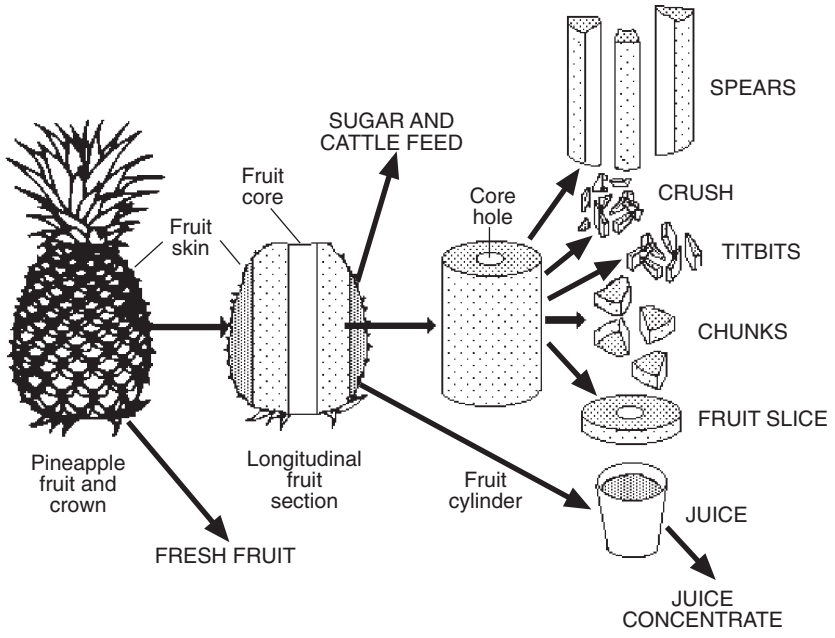

Fig. 1.2. Pineapple products.

Table 1.1. Pineapple production (t), ha harvested and yields (t ha^{-1}) for 2001 by country (Anon., 2002).

Country	Production (t)	Harvested (ha)	Yield (t ha^{-1})
Thailand	2,300,000	97,300	24
Philippines	1,571,904	45,000	35
Brazil	1,442,300	59,238	24
China	1,284,000	57,700	22
India	1,100,000	80,000	14
Nigeria	881,000	115,000	8
Mexico	535,000	12,500	43
Costa Rica	475,000	12,000	40
Colombia	360,000	9,000	40
Indonesia	300,000	42,000	7
Venezuela	300,000	15,000	20
USA	293,000	8,130	36
Kenya	280,000	8,500	33
Côte d'Ivoire	225,675	5,200	43
South Africa	145,441	6,200	23
Australia	140,000	3,000	47
Dominican Republic	136,862	5,500	25
Malaysia	130,000	7,000	19
Guatemala	101,287	3,710	27
Honduras	70,000	3,900	18
Cameroon	42,000	4,000	11
Martinique	20,800	484	43
Swaziland	19,680	600	33
Cuba	19,000	400	48
Cambodia	16,500	1,600	10
Puerto Rico	15,000	500	30

Philippines of both processed and fresh fruit are frequently handled with other products, such as bananas. The large scale of production, high level of technology and low labour costs make competition with production, processing and marketing of both canned and fresh fruit from Thailand and the Philippines very difficult for the smaller producing countries. Australia and South Africa market canned and fresh fruit almost exclusively within the country and remain competitive because of efficient production and processing (Sanewski and Scott, 2000) and international trade barriers. While Hawaii was the centre of world processing and technology in the first half of the 20th century, its proportion of production has declined steadily as production and competition from Thailand and the Philippines have risen (Fig. 1.3). However, the value of the Hawaiian pineapple industry (US$) unadjusted for inflation has increased as production was gradually shifted from processed to fresh fruit for the domestic market (Rohrbach, 2000). Taiwan (Lin and Chang, 2000), like Hawaii, has shifted from a dominant processing industry to a domestic and export fresh-fruit market.

World trade in pineapple mainly consists of processed products. World exports of canned pineapple doubled between 1983 and 1992, passing 1 million t and representing a value of more than US$600 million. Asian countries have been the primary suppliers, increasing their share from 69 to 85%, while Africa's share has decreased from 25 to 10%. Leading countries are now Thailand (315,000 t), the Philippines (209,000 t), Indonesia (95,000 t), Kenya (84,000 t) and Malaysia (44,000 t). The European Union imports 450,000 t, a 2.4-fold increase between 1983 and 1993. The USA and Canada import

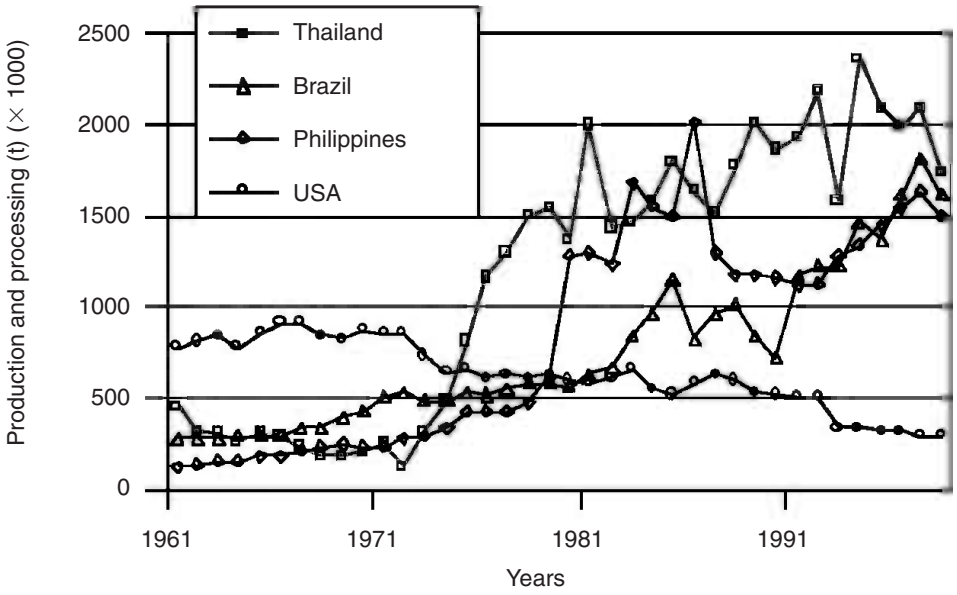

Fig. 1.3. Shifts in Hawaiian and multinational foreign production and processing industries (Anon., 1998a; Baker, 1990).

380,000 t, representing a replacement for decreasing Hawaiian production (Loeillet, 1995; Anon., 1998a).

The market for concentrated pineapple juice, especially frozen concentrate, has also increased. Estimated at 40,000 t in 1983, it increased to 167,000 t in 1993 (representing then up to US$400 million), to reach 215,000 t in 1993. Supply is dominated by Thailand and the Philippines. The Philippines is also largely dominant for the smaller market for single-strength juice (70,000 t). The USA and Canada (90,000 t) are the major importers of concentrated juice, with Europe (118,000 t) second (Loeillet, 1994).

Per capita consumption of pineapple juice in the USA is essentially static at between 1 and 1.3 l $year^{-1}$ which contrasts with increases of both orange- and apple-juice consumption (Fig. 1.4).

The international fresh-pineapple market (about 670,000 t) is dominated by Costa Rica, the Philippines and the Côte d'Ivoire. The North American market is primarily supplied by Costa Rica and Hawaii (Fig. 1.5). In the USA, annual per capita consumption of fresh pineapple fruit has gone from 0.3 to 0.9 kg. This is still very low when compared with the approximately 5 kg consumption of processed pineapple over the past 25 years (Fig. 1.6) and with the consumption of other fruits such as bananas, apples and oranges (Fig. 1.7). The European market is mainly supplied by Côte d'Ivoire, with significant amounts transshipped through France to several other European countries (Fig. 1.8; Aldrich, 1984; Anon., 1998b). European countries such as the Netherlands and Belgium obtain fresh pineapple from several different countries, including Costa Rica, as well as the Côte d'Ivoire through France. In Europe, per capita consumption of fresh pineapple is highest in France and in 1984 was approximately equal to the current US fresh-pineapple consumption (Aldrich, 1984). The principal South-East Asian fresh-fruit export market is Japan, which is dominated by the Philippines. Taiwan also supplies significant amounts. China, Indonesia and Hawaii occasionally supply

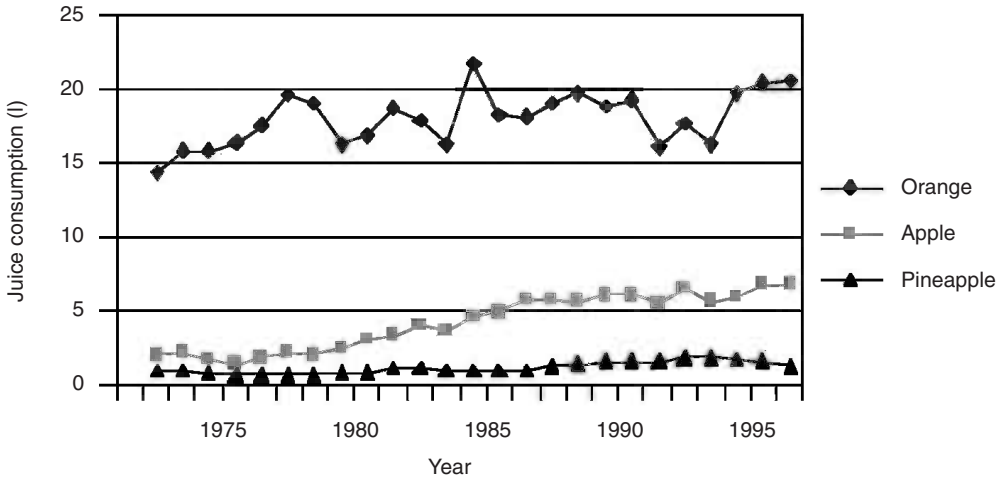

Fig. 1.4. Per capita consumption of orange, apple and pineapple juice in the USA (Putnam and Allshouse, 1999).

small amounts. Imports of fresh pineapple into Japan have declined somewhat in recent years (Fig. 1.9) (Anon., 1997). In contrast to Europe and the USA, Brazil's consumption of fresh pineapple is approximately 11 kg per capita year^{-1} (Reinhardt and Souza, 2000).

Chilled fresh-cut fruit pineapple packed as spears or chunks in sealed plastic bags for retail sale is a relatively new product. Fruit may be processed at the production site and transported chilled at 0–1°C or shipped whole without the crown to large metropolitan centres and processed just before retail sales. The shelf-life of this product is limited to 1–3 weeks unless the product is actually frozen. The chilled fresh-cut product addresses consumer demand for ready-to-eat foods that do not require any preparation time. Industry sources estimate that the market for vacuum-packed fresh-cut pineapple in Japan will soon

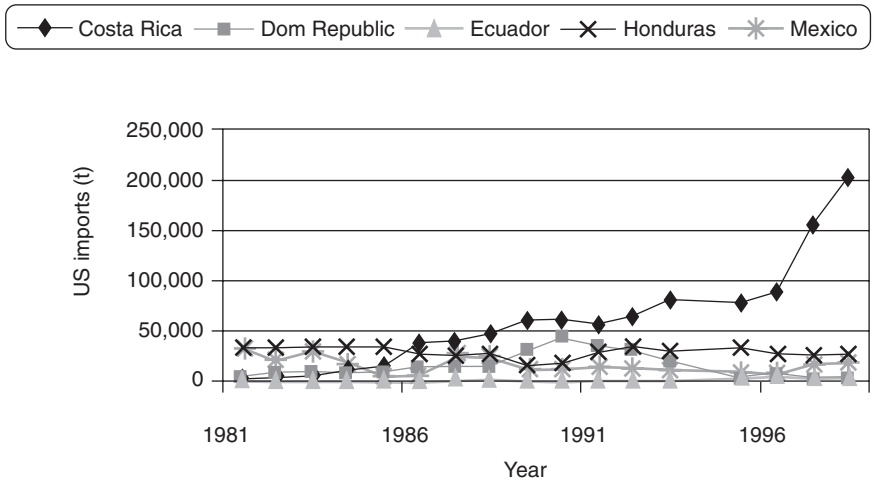

Fig. 1.5. Countries supplying fresh pineapple to the US market (Anon., 1998b). Dom, Dominican.

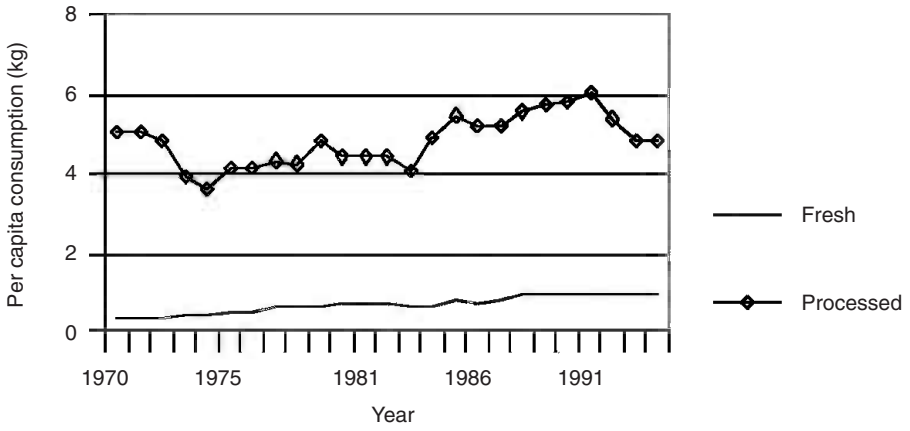

Fig. 1.6. Per capita consumption of fresh and processed pineapple in the USA (Putnam and Allshouse, 1999).

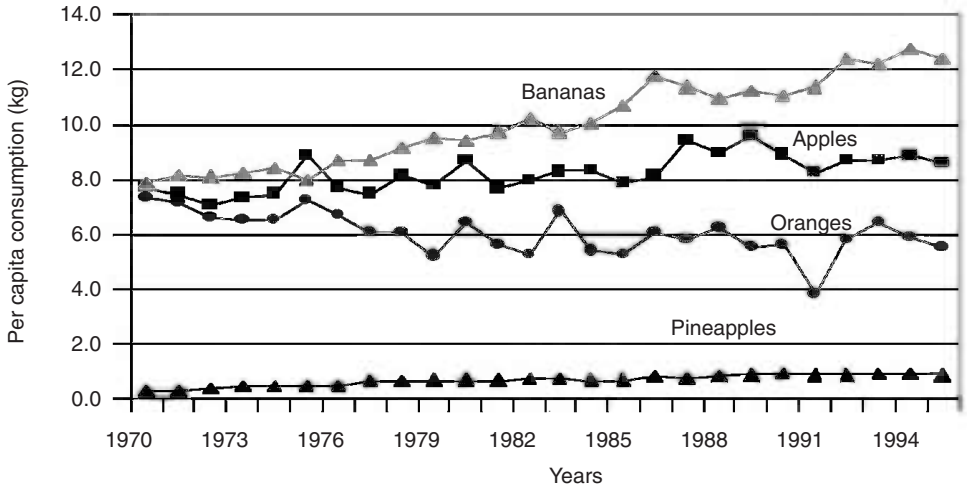

Fig. 1.7. Per capita consumption of bananas, apples, oranges and pineapple in the USA (Putnam and Allshouse, 1999).

approach 20% of the total fresh-pineapple fruit market for Japan (Anon., 1999). In Hawaii, it is estimated that chilled fresh-cut pineapple represents up to 10% of the total fresh-fruit market. High-pressure processing has recently been used to extend the shelf-life of chilled fresh-cut fruit (Aleman *et al.*, 1994). Commercialization of this process will be dependent on the costs versus benefits of high-pressure processing equipment.

Most of the world production (about 70%), and most of the canned pineapple (about 95%), comes from the cultivar 'Smooth Cayenne'. 'Queen' is present in small specific niches of high-quality and expensive fresh fruit (Loeillet, 1996). The increasing importance of fresh pineapple in the temperate markets is putting pressure on the multinational corporations to switch to cultivars that are superior to 'Smooth Cayenne' as fresh fruit. As industries shift to domestic fresh-fruit markets because of competition in processed fruit, 'Smooth Cayenne' does not provide today's consumer with the

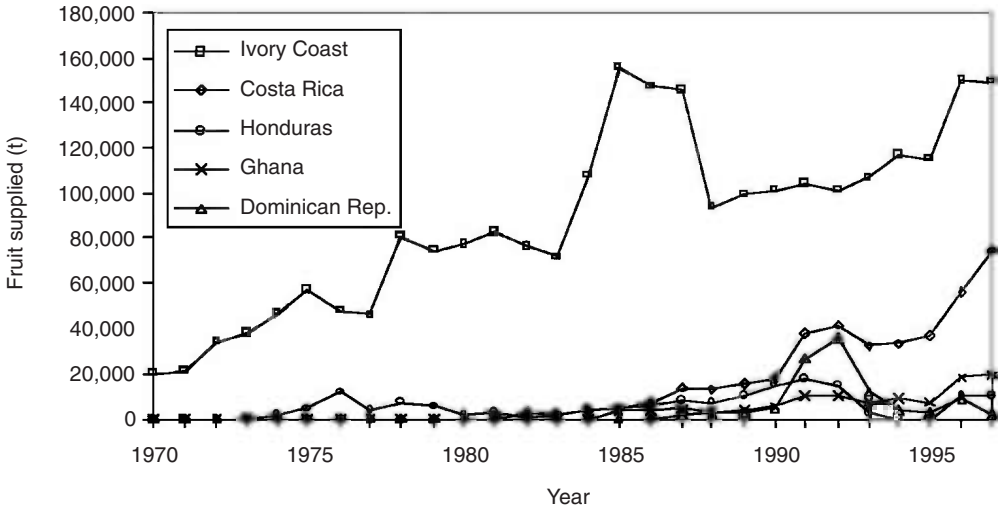

Fig. 1.8. Major countries supplying fresh fruit to the European market (Anon., 1998b; Loeillet, 1994).

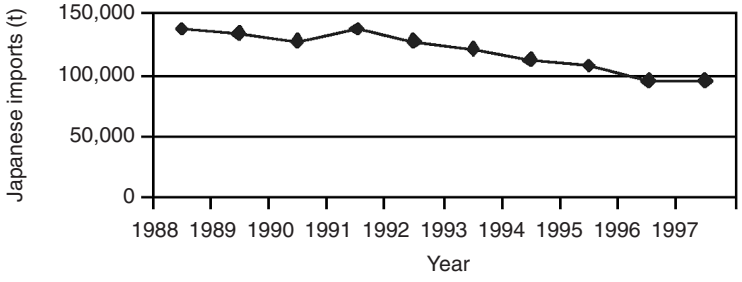

Fig. 1.9. Metric tons of pineapple imported into Japan (Anon., 1997, 1999).

best fruit quality (Paull, 1993; Sanewski and Scott, 2000). Taiwan, Hawaii, Malaysia, Australia, Cuba, Brazil and the French are putting resources into developing cultivars specifically for domestic fresh-fruit markets. A first result of these efforts has been the recent and successful introduction of a low-acid cultivar by Del Monte from Costa Rica into the European and American markets (Malezieux, 2000).

By-products

Portions of the pineapple plant and processing wastes, in the form of shell and core materials, and centrifuged solids from juice production have been evaluated and used as animal feeds (Wayman *et al.*, 1976; Olbrich and Al, 1977; Stanley and Ishizaki, 1979). In many countries, feed tolerances must be established for pesticides used during production in order for by-products to be used as animal feeds. The requirements for tolerances affect the economic viability of by-product use for feeds, even though a disposal cost exists for cannery wastes. Additionally, because of the low nutrient values of pineapple by-products, animal weight gains may not be economical when higher-quality feeds are available.

Pineapple fibre is considered to be more delicate in texture than any other vegetal fibre. About 60 cm long, white and creamy

and lustrous as silk, it easily takes and retains dyes. Numerous tests in Brazil, Florida, India and the Philippines have shown its exceptional resistance to salt, vapour and traction (Correa, 1926; Montinola, 1991). However, while small cottage industries exist for speciality uses of pineapple fibre from particular cultivars, numerous attempts at commercial production as a subproduct of the fruit industry have failed. In fact, fibre quality and yield are highly dependent on the cultivar, and those of 'Smooth Cayenne' are among the weakest. In addition, cultural practices for fruit production have detrimental effects on fibre characteristics. Pineapple fibre has also been processed into paper, which shows remarkable thinness, smoothness and pliability (Collins, 1960; Montinola, 1991). Recent studies have resulted in several patents on paper production and the development of low-density polyethylene composites (Fujishige *et al*., 1977; Fujishige and Tsuboi, 1978; George *et al*., 1993, 1995).

Bromelain was originally only extracted from Hawaiian pineapple stems but now is manufactured in Taiwan, Thailand, Brazil and Puerto Rico. The variability in the commercially produced product and its multiple ingredients have limited successful development. Pineapple bromelain has been used commercially as a meat-tenderizing enzyme and as a nutraceutical. Attempts have been made to develop bromelain for pharmaceutical use. The complexity of the active components of bromelain has limited pharmaceutical research. Bromelain has shown the following activity: (i) interference with the growth of malignant cells; (ii) inhibition of platelet aggregation; (iii) fibrinolytic action; (iv) anti-inflammatory processes; and (v) skin débridement (Lotz-Winter, 1990). These biological properties of bromelain have potential therapeutic activity in: (i) tumour growth; (ii) blood coagulation; (iii) inflammatory changes; (iv) débridement of severe burns; and (v) enhancement of drug absorption (Taussig and Batkin, 1988).

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2 Morphology, Anatomy and Taxonomy

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Morphology

Ananas comosus is a herbaceous perennial of the *Liliopsidae* (monocotyledonous), whose terminal inflorescence gives origin to a multiple fruit (sorose). After maturation of the first fruit, the plant develops new shoots from axillary buds, so producing new growth axes capable of producing another fruit. The same plant may thus give a sequence of various production cycles. In most commercial plantings, the plants are not allowed to produce more than two to three crops, due to a reduction in fruit size and uniformity. Then a new plantation must be regularly established. This may be done with the same lateral shoots of the preceding crop, or with other vegetative propagules, such as the fruit crown, or, in many cultivars, slips produced along the peduncle. This vegetative reproduction is also dominant in wild pineapples, where, in addition to lateral shoots, the crown and slips contribute to propagation as they resume rapid growth at fruit maturity. The long peduncle then bends because of this mass and the crowns and slips reach the ground and may root. Thus most natural populations appear to consist of a single clone, expanding as if propagating by stolons.

The adult plant is 1–2 m high and 1–2 m wide, and it is inscribed in the general shape of a spinning top. The main morphological structures to be distinguished are the stem, the leaves, the peduncle, the multiple fruit or syncarp, the crown, the shoots and the roots (Fig. 2.1). The following description is mainly focused on the cultivated pineapple. It is partly based on the anatomical studies of Krauss (1948, 1949a,b) and Okimoto (1948).

Stem

The pineapple stem is club-shaped, with a length of 25–50 cm and a width of 2–5 cm at the base and 5–8 cm at the top. Its aerial part is straight and erect, while the shape of the earthed part depends on the material used for planting. It is markedly curved when coming from a slip, as the stems of these propagules are comma-shaped, less curved when coming from a stem shoot and erect when coming from a crown. Nodes can be visualized by the leaf scars left after stripping the leaves from the stem. Internodes are short (1–10 mm according to their position), so the whole rosette appears dense and compact. Flattened shoot buds, 3–5 mm high and about 5 mm wide, occur in the leaf axils. In the central portion of the stem, they are larger because of an increase in the size of their prophyll (the first leaf of the shoot, which encloses it). A striking feature of the pineapple stem is the presence of adventi-

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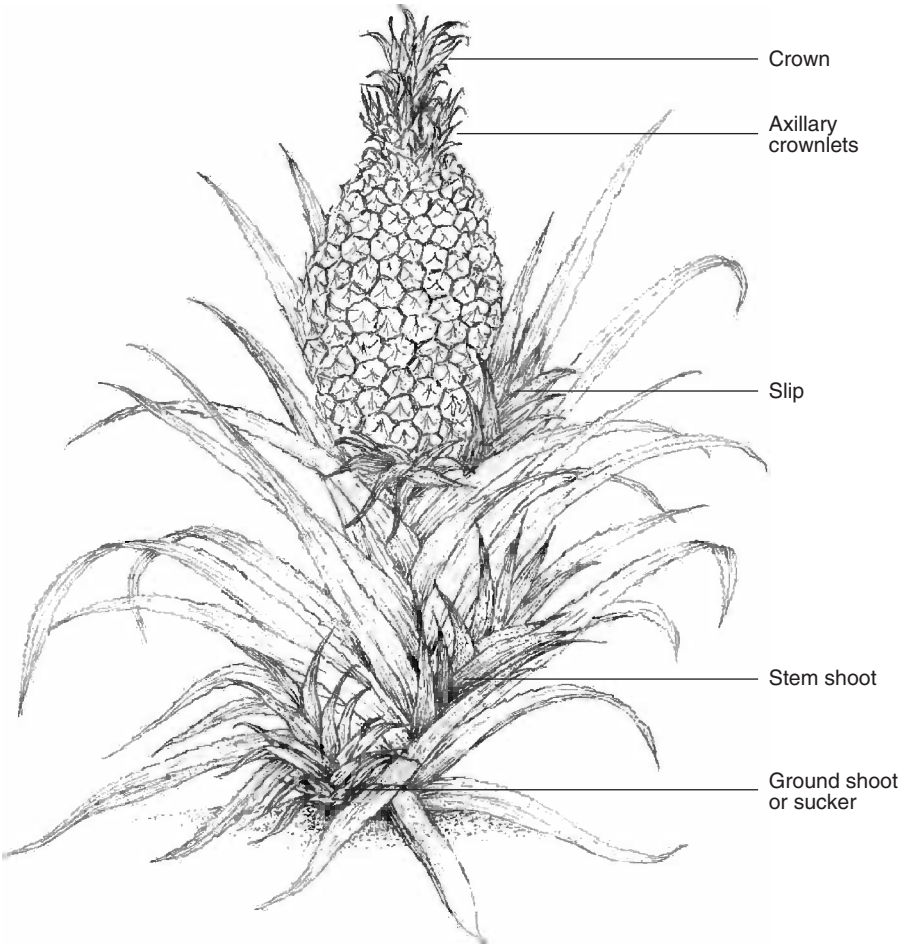

Fig. 2.1. Main morphological structures of the pineapple plant.

tious roots breaking through the epidermis, and growing flattened and distorted, tightly wound around the stem, between the leaves. Their older portion is suberized. These aerial roots rarely produce laterals. They are elongated from a few millimetres in the subapical region to 10 cm or more near the stem base. Thus, the underground portion of the stem is covered with a tuft of adventitious fibrous roots.

The stem (Fig. 2.2) constitutes a central cylinder, or stele, and a cortex, separated by a thin layer of vascular bundles produced by the dome-shaped apical meristem. The dense network of vascular tissue separating cortex and stele consists chiefly of xylem, with very little phloem. In this tissue, areas of non-vascular tissue, or leaf gaps, are disposed at intervals, allowing leaf-trace bundles to pass from the cortex into the stele. This vascular cylinder is thicker and suberized at the stem base. On the cortical side, a narrow layer of long, thin-walled cells bound it. Vascular bundles are very numerous throughout the stem but less so in the cortex than in the stele. The latter is mainly constituted of a compact parenchyma with abundant starch. It contains large cells with raphides of calcium oxalate crystals. The cortex is composed of a parenchymatous tissue, crossed by the isolated vascular bundles going to the leaves, of the adventitious roots

originating at the boundary with the central cylinder and of circumferential small bands of vascular tissue lying just above the leaf attachment to the stem. The inner parenchyma of this cortex is also rich in starch and contains raphide cells. Limiting the stem externally is the epidermis, with peltate trichomes in the nodal regions.

Leaves

The sessile leaves enclose the stem on two-thirds of its circumference. The phyllotaxy varies, being 5/13 in large-fruited cultivated pineapples and 3/8 in small-fruited wild pineapples (Kerns *et al.*, 1936). Leaf number is variable between cultivars but generally around 40–80. The lower ones, originating from the planting material or produced soon after planting, are smaller (5–20 cm) compared with the younger ones, which can reach more than 1.6 m in length and 7 cm in width, depending on the cultivar and ecological conditions. The apical ones are short and erect. The leaves are ensiform and, except for the young apical ones, broader at their base, which forms a non-chlorophyllous sheath around the stem. The blades then taper progressively to a sharply pointed indurated tip. The constriction between the sheath and the blade is more marked in certain wild pineapples. Temporary stress during leaf growth may cause variations in width or spininess, or both, along the blade. Leaves are semi-rigid, thanks to their crescent-shaped section. As in other bromeliads, this allows the plant to collect water in the rosette, where it can be absorbed by the aerial roots present along the stem or through the epidermis of the sheath. The concave adaxial face is green or dark green, with some anthocyanins, to dark red or purple, according to the cultivar and conditions. The abaxial side is convex, with a surface corrugated by longitudinal grooves. Both sides are covered by peltate trichomes,

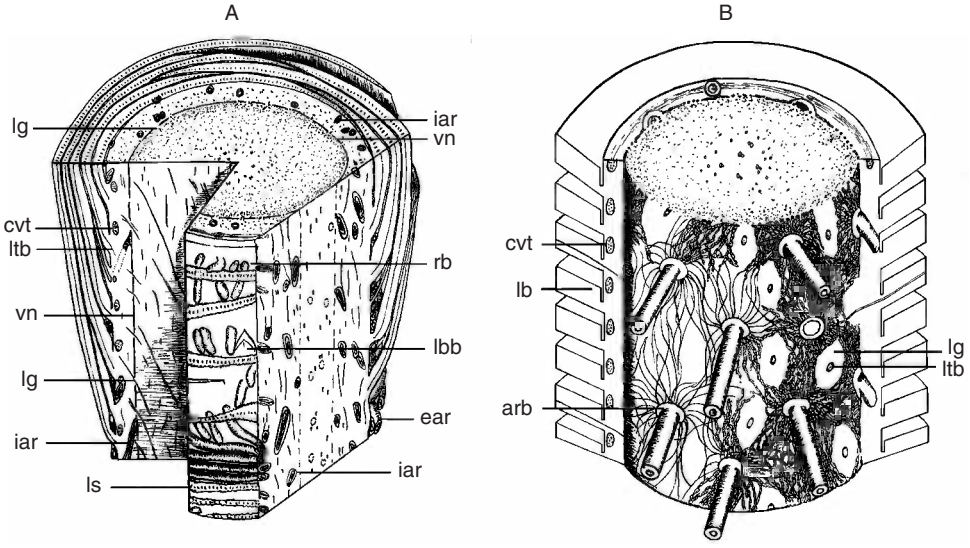

Fig. 2.2. A. Central region of the 'Smooth Cayenne' pineapple stem cut to show transverse, radial and tangential views of gross external and internal structure. Tangential section cut at boundary between cortex and stele. iar, internal, and ear, external portions of adventitious roots; cvt, circumferential band of vascular tissue; vn, vascular network at the boundary between cortex and stele; lg, leaf gap; ltb, leaf-trace bundle; ls, leaf scar; lbb, lateral branch bud; rb, tip of emerging root, commonly called a root 'bud'. B. Diagrammatic representation, showing portion of the cortex cut away to expose the vascular network at the boundary between cortex and stele, and xylem elements from roots. arb, adventitious root base; cvt, circumferential band of vascular tissue; lb, leaf base; lg, leaf gap; ltb, leaf-trace bundle. (After Krauss, 1948.)

particularly the abaxial one, which is densely furfuraceous and silvery (see Fig. 5.7). The leaf margins are usually thorny; however, certain cultivars are partially or totally inermous. In some smooth cultivars, the lower epidermis is folded over the leaf edge and extended over the upper surface, so producing a narrow silvery stripe, a trait called 'piping' by Collins (1960).

A section across the leaf (Fig. 2.3) shows successively a thick and smooth cuticle; a particular upper epidermis, which consists of a single layer of cells, each containing a silica body, orientated perpendicularly to the leaf axis, and rigidified by thick and undulated lateral and inner cell walls; the hypodermis; the water-storage tissue, consisting of various layers of thin-walled cells, which accounts for a quarter to half of the leaf thickness, depending on the water status of the plant; the chloroplast-rich mesophyll, with the vascular bundles, fibre strands and aerating canals; and the lower hypodermis and epidermis, with the stomata arranged longitudinally along the characteristic grooves of the abaxial leaf side, covered by numerous trichomes, giving it a silvery appearance and increasing reflectance. The fibre strands confer a high tear resistance to the pineapple leaves. Stomatal density is rather low, about 80 stomata mm^{-2}. The trichomes, present in almost all the known bromeliads, are flat and shield-shaped, parallel to the leaf surface. They consist of a central disc of live cells, an outer ring of dead cells and a pluricellular stalk arising from the epidermis and subepidermis. Like the stomata, they are nested in small cavities along the bottom of the underside furrows, with their broad heads spreading out to virtually cover the entire leaf surface. In many bromeliad species, the dead cells can absorb water and nutrients and the stalk can carry them into the inner leaf tissues. The shield also acts as a plug, closing the concavity where the stalk is inserted and protecting it from drying out. These trichomes function as one-way valves, playing an important role in the capacity of bromeliads to improve and maintain their water status (Benzing, 1980). However, the pineapple trichomes appear to be hydrophobic and do not absorb water (Krauss, 1948, 1949a,b). The presence of large numbers of mitochondria in the stalk cells give indirect evidence for an important role in uptake of dissolved nutrients (Sakai and Sanford, 1980). Another important role is to protect the plant from excessive transpiration and intense sunlight. More generally, the thick cuticle, the water-storage tissue, the disposition of the stomata, the trichomes and the crassulacean acid metabolism (CAM) all contribute to the remarkable water economy of pineapple.

Roots

Primary roots are only found in very young seedlings. They die soon after germination and are replaced by the adventitious roots. These form a short and compact system at the stem base, with numerous strong roots and limited branching. Under ideal conditions, the soil root system may spread up to 1–2 m laterally and 0.85 m in depth. The number of roots produced after planting is positively correlated with shoot weight, and crowns produce more roots than do shoots. The root internal anatomy is typical of monocots, with, towards the centre: the epidermis, with root hair cells; the cortex comprising the exodermis, the outer cortex, with sclerenchyma and aerating canals, and the inner cortex, with a lagunar parenchyma; the endodermis, pericycle, vessels and pith (Fig. 2.4). Their most characteristic trait is the medullar structure given by the aerating canals, formed by the tip-to-tip junction of raphide cells in the outer cortex, and by the air lacunae formed by the disappearance of thin-walled cell groups. Branch roots originate in the pericyclic region of the main roots.

Inflorescence and fruit

The peduncle and inflorescence develop from the apical meristem, the diameter of which is suddenly increased until the initiation of the peduncle (Kerns *et al.*, 1936). The stage of inflorescence emergence is called 'red heart' because of the five to seven reddish peduncle bracts at its base. These bracts

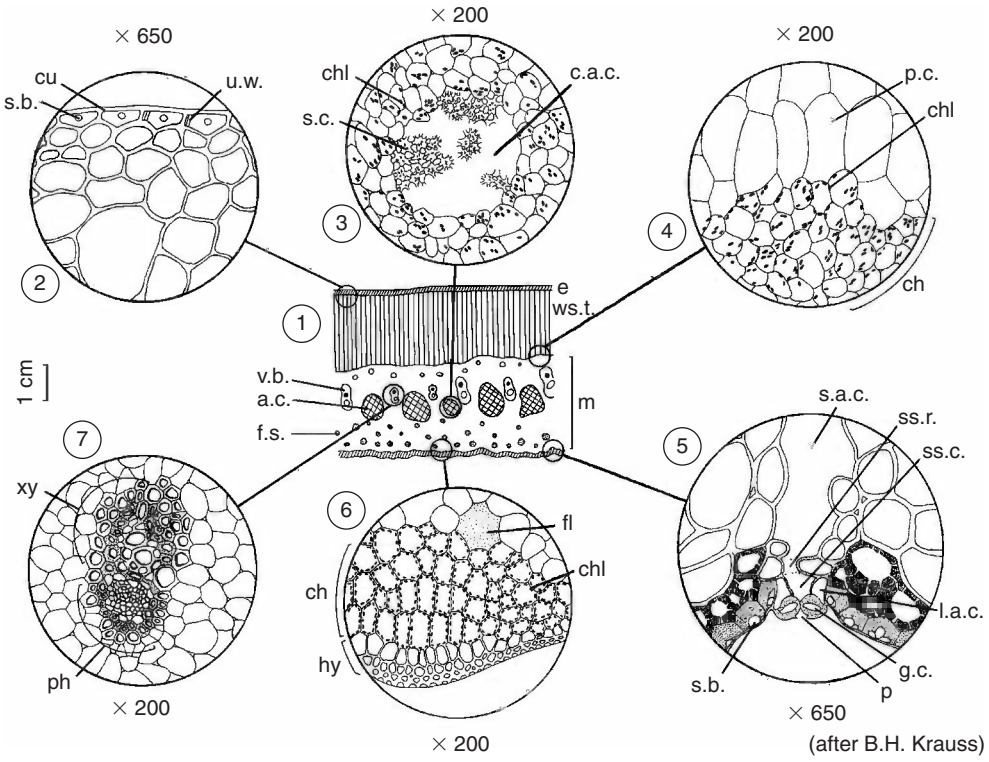

Fig. 2.3. 1. Diagram of a transverse section of a 'Smooth Cayenne' leaf showing: a.c., aerating canal; f.s., fibre strand; e, epidermis; v.b., vascular bundle; m, mesophyll; ws.t., water-storage tissue. 2. Outer epidermis showing: cu, cuticle; s.b., silica body; u.w., undulating wall. 3. Aerating canal showing: c.a.c., central aerating canal; s.c., stellate cell; chl, chloroplast. 4. Lower boundary of water-storage tissue showing: ch, chlorenchyma; chl, chloroplast; p.c., palisade cells of water-storage tissue. 5. Lower epidermis showing: ss.r., substomatal ring; s.a.c., secondary aerating canal; l.a.c., lateral accessory cell; g.c., guard cell; ss.c., substomatal chamber; s.b., silica body; p, pore. 6. Hypodermis and mesophyll (trichomes not shown) showing: ch, chlorenchyma; chl, chloroplast; fi, fibres; hy, hypodermis. 7. Vascular bundle (mesophyll without chloroplasts) showing: ph, phloem; xy, xylem. (After Py *et al.*, 1987, with permission.)

are shorter and narrower than the ordinary leaves. The peduncle elongates after flower formation. Its length varies widely with the botanical varieties or even cultivars. In addition to its bracts, it bears, in many cultivars, a variable number of slips (up to a dozen or more), which can be positioned more or less regularly between the stem and the fruit, at the axis of the peduncle bracts, or grouped just beneath the fruit. These slips can be considered as dwarfish 'aborted' fruits with a relatively large crown (Collins, 1960). They may constitute an appreciable source of planting material in extensive cultivation systems.

The inflorescence consists of fewer than 50 (in some wild clones) to more than 200 (in some cultivars) individual flowers; it is capped by a crown, composed of numerous short leaves (up to 150) on a short stem. The flowers or individual fruits are disposed around the central axis according to an 8/21 phyllotaxy in large-fruited cultivated pineapples (M.B. Linford, cited by Kerns *et al.*, 1936) and a 5/13 phyllotaxy for small-fruited wild pineapples or for young cultivated pineapples flowering prematurely (Kerns *et al.*, 1936). The fibrous axis containing the many vascular bundles that supply

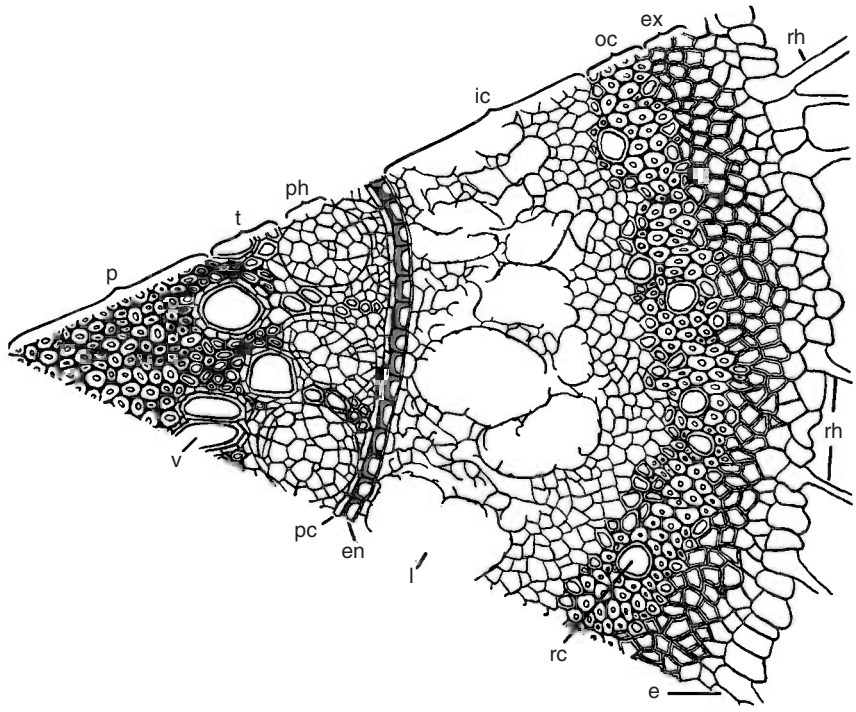

Fig. 2.4. Transverse section of a mature root of 'Smooth Cayenne' pineapple showing: e, epidermis; ex, exodermis; oc, outer cortex with raphide cells (rc), whose transverse walls are collapsed to form air passages; ic, outer portion of inner cortex; t, tracheids; ph, phloem; p, pith; v, vessel; pc, pericycle; en, endodermis; l, large lacunae formed by collapse of many cells of inner cortex; rh, root hairs. (After Krauss, 1949b. © The University of Chicago, all rights reserved.)

the flowers is continuous with the peduncle and with the short stem of the crown (Fig. 2.5). Between the uppermost flower and the crown is a transition region with bracts but no flowers. The edible part of the fruit consists chiefly of the ovaries, the bases of sepals and bracts and the cortex of the axis. The fruit shell is composed chiefly of sepal and bract tissues and the apices of the ovaries (Okimoto, 1948). Anthesis normally takes place within a day. Flowering lasts 10–15 days and occurs in a more or less acropetal succession along the inflorescence axis, but some cultivars flower in a very disorderly manner.

Flowers are hermaphroditic and trimerous, with three sepals, three petals, six stamens in two whorls of three and one tricarpellate pistil (Fig. 2.6). The anthers are bilobed, introrse and dorsifixed. The hollow, trilobed and trifid style is almost as long as the petals and equal to or longer than the stamens. At anthesis, each stylar canal is an unobstructed open channel from the stigma to the locule directly above the placenta. Petals are ligulate and free, each bearing at its base two slender funnelform scales or, more rarely, lateral folds that overlap the filaments. Petals are white at their base to violet-blue at their tip. They are so close together at their outer end that only small insects can enter the flower. This narrow tubular flower and the abundant nectar production are particularly adapted to hummingbird pollination. Indeed, the three large nectary glands are so productive that nectar often fills the corolla and seeps out. The sepals are deltoid and appear similar to the bracts in colour and texture. Each flower is surrounded and subtended at its base by a pulpous and thick

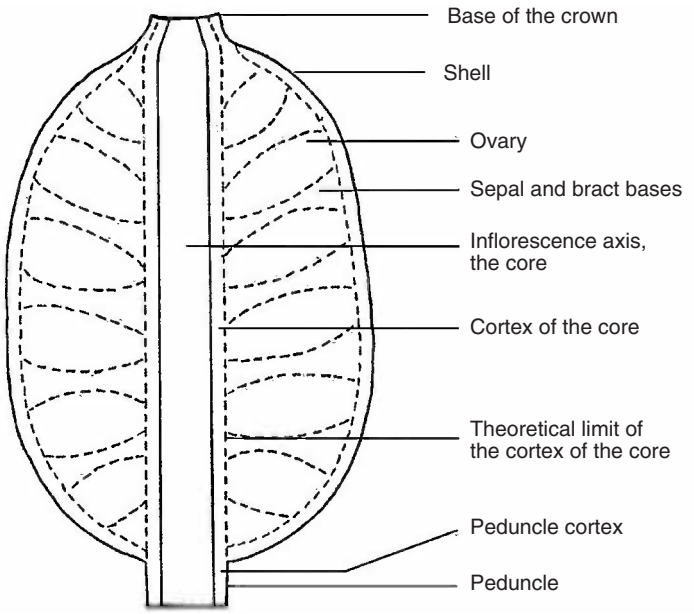

Fig. 2.5. The morphology of a 'Smooth Cayenne' pineapple fruit. (After Okimoto, 1949. © The University of Chicago, all rights reserved.)

bract, covered by trichomes, which becomes pointed and papyraceous at its tip. Parts of three other bracts complete the enclosure of the flower. Bract spininess is correlated with leaf spininess.

In the syncarpic inflorescence resulting from the fusion of the basal part of the flowers and their axis, ovaries of adjacent flowers are separated by the parenchymatous tissue of the calyx and bract bases. The ovary is inferior, tricarpellate and trilocular, with the three septa forming an inverted Y when seen in tangential section of the inflorescence. The placentae and ovules are located in the upper part of three deep cavities, called locules, which are separated by the nectary glands. The ovules are caudate and arranged in two single or double rows. The number of ovules per flower varies with the cultivars, from 16 to 71 (Coppens d'Eeckenbrugge *et al.*, 1993). The occurrence of two types of ovules (unitegmic orthotropous and bitegmic anatropous) within the same ovary is common and orthotropous ovules are fertilized (Okimoto, 1948; Rao and Wee, 1979; F. Van Miegroet, 1993, personal communication). Orthotropous ovules are much less frequent than anatropous ovules and their presence and numbers are a varietal characteristic (M.F. Duval and G. Coppens d'Eeckenbrugge, unpublished results). Pollen grains are prolate and spheroidal, biconvex, isopolar and bilaterally symmetrical and diaperturate, with circular to slightly elongated apertures situated at the poles. The equatorial (36–51 μm) and polar (46–59 μm) dimensions are variable. The exine is reticulate, and the polar areas show finer reticulation than the rest of the surface (Wee and Rao, 1979). Male and female gametogenesis and embryogenesis are revised by Chan *et al*. (Chapter 3, this volume).

There is no floral abscission, and, except for the withering of the style, stamens and petals, the entire blossom develops parthenocarpically into a berry-like fruitlet. In the cultivated pineapple, growth from blossoming inflorescence to mature fruit results in a 20-fold increase in weight. The enlargement of the calyx results from continued growth by cellular division, in stages up to flowering, and cell enlargement, in the

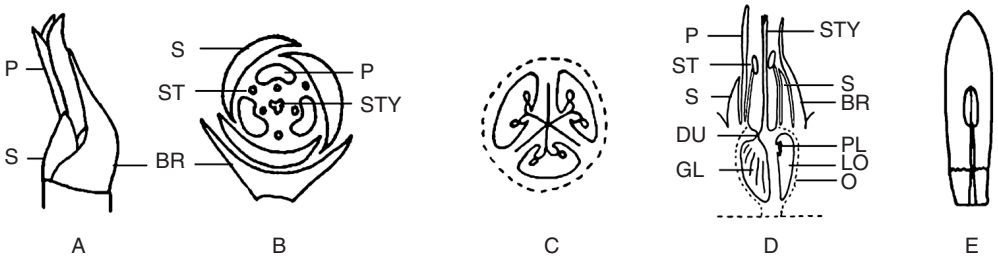

Fig. 2.6. Pineapple flower. A. Floral diagram. B. Flower and subtending bract. C. Cross-section of ovary at placenta level. D. Longitudinal section. E. Petal with scales and opposite stamen. BR, subtending bract; DU, nectary duct; GL, septal gland; LO, locule; O, ovary limit; P, petal; PL, placenta; S, sepal; ST, stamen; STY, style. (After Okimoto, 1949. © The University of Chicago, all rights reserved.)

later stages. During this size increase, cell walls get thinner. The bract, sepal and ovary tissues are prominent structures in the mature fruit. The large, conspicuous bract is fleshy and widened at its base and bends over the flattened calyx surface, covering half of the fruitlet. Its papery tip dries during maturation. Internally, the locules get longer but relatively narrower and less conspicuous in the developed fruit because of the expansion of adjacent tissues, especially of the septa. Placentas show some enlargement but far less than the septal tissues, unless they bear mature seeds. The seeds are approximately 3–5 mm long and 1–2 mm wide, flat on one side and curved on the other, with a pointed end. They contain a hard flinty endosperm and a minute embryo enclosed in a brown to black coat, extremely tough and leathery and roughened by numerous longitudinal ridges (Miles Thomas and Holmes, 1930). In the mature fruit, the stylar canals get completely closed, first by a mucilaginous plug, soon after anthesis, and a week or two later by cellular occlusion.

Vegetative propagules

Vegetative propagules are classified according to their position on the plant. Suckers appear on the earthed part of the stem. Stem shoots, which appear on the aerial part, are more frequent. Slips appear on the peduncle. They are often grouped near the base of the fruit. Sometimes, they are produced from the basal eyes of the fruit (collar of slips). Slips are curved at their base. As they are numerous in most cultivars, they are useful for rapid propagation. The crown can also be used for planting when the pineapple fruit is processed. Some plants may lack a crown or, on the contrary, produce multiple crowns. Also, crownlets may grow at the base of the main crown or from some of the upper fruitlets.

Taxonomy

The *Bromeliaceae*

Pineapple belongs to the order *Bromeliales*, family *Bromeliaceae*, subfamily *Bromelioideae*. With 2794 species among 56 genera, according to Luther and Sieff (1998), this is the largest family whose natural distribution is restricted to the New World, with the exception of *Pitcairnia feliciana* (Aug. Chev.) Harms & Mildbr., which is native to Guinea. Their unified geographical distribution and their strong adaptation towards an epiphytic mode of life indicate that this is quite a young family. On the other hand, morphologically they seem older than *Rapateaceae*, which led Smith (1934) to accept that their restriction to the Americas does not indicate extreme youth. Judd *et al*. (1999) consider that the family probably represents an early divergent clade within the superorder *Commelinanae*. The *Bromeliaceae* have adapted to a very wide range of habitats, ranging from terrestrial to

epiphytic, deep shade to full sun, mesic to extremely xeric and sea level to alpine, and from the hot and humid tropics to the cold and dry subtropics. They thus cover a wide area, from the centre of the USA to the northern regions of Argentina and Chile (Smith, 1934). The *Bromeliaceae* are set apart from other monocots by the unique, stellate or scale-like multicellular hairs and the unusual conduplicate, spiral stigmas (Gilmartin and Brown, 1987). They are also characterized by a short stem, a rosette of narrow stiff leaves, terminal inflorescences in the form of racemes or panicles, hermaphroditic and actinomorphic trimerous flowers with well-differentiated calyx and corolla, six stamens and superior to inferior trilocular ovary, with axile placentation and numerous ovules. Fruits are capsules or berries and contain small naked, winged or plumose seeds, with a reduced endosperm and a small embryo. Most species are epiphytic or saxicolous, but some are terrestrial. They are particularly adapted to water economy, based on: (i) rosette structure; (ii) ability to absorb water and nutrients through their waxy leaves and aerial roots; (iii) ability to store water in specialized aquiferous leaf tissue; (iv) multicellular trichomes functioning as water valvulae and reflecting radiation; (v) a thick cuticle; (vi) location of stomates in furrows, limiting evapotranspiration; and (vii) CAM. Their root system is not well developed and functions mostly to anchor the plant.

The *Bromeliaceae* are divided into three subfamilies, the *Pitcarnioideae*, the *Tillandsioideae* and the *Bromelioideae*. While this division is widely recognized, their phylogenetic study has been confounded by high levels of homoplasy for morphological and ecological characters. Most experts agree that certain attributes have arisen several times independently as adaptations to their extreme environment. Molecular studies have given contradictory results, placing different subfamilies at the base of the *Bromeliaceae* (Clark and Clegg, 1990; Givnish *et al*., 1990; Ranker *et al*., 1990; Terry *et al*., 1997). The *Pitcarnioideae* were long held to be the most archaic. They are almost terrestrial, with armed leaf margins, hypogenous or epygenous flowers and dry dehiscent capsules containing naked or appendaged seeds adapted to wind dispersal. Their monophyly is now questioned and new subfamilies could be defined (Ranker *et al*., 1990; Terry *et al*., 1997). The subfamilies *Tillandsioideae* and *Bromelioideae* are considered monophyletic. The former include mostly epiphytic species, with smooth leaf margins, flowers usually hypogenous and dry dehiscent capsules containing many plumose seeds adapted to wind dispersal. The second is the most numerous. Most *Bromelioideae* are epiphytic, frequently spiny, with epigynous flowers and fleshy or leathery berries containing naked seeds as an adaptation to dispersion by birds or mammals. All the species examined exhibit CAM, with the exception of those of the genus *Greigia*, a trait much less frequent in the other subfamilies (Medina, 1990). They seem to have evolved from eastern Brazil and the Amazon basin, and they show a tendency to fusion of parts, fusion of their carpels to make an indehiscent fruit, formation of an inferior ovary and fusion of sepals, petals and filaments. As stated by Smith (1934), '*Ananas* capped the fusion tendency by merging the whole inflorescence, flowers, bracts and all into one massy compound fruit.'

Pineapple is by far the most important economic plant in the *Bromeliaceae*. However, in the same *Bromelioideae* subfamily, some *Aechmea* and *Bromelia* species also yield edible fruits, such as *A. bracteata* (Swartz) Grisebach, *A. kuntzeana* Mez, *A. longifolia* (Rudge) L.B. Smith & M.A. Spencer, *A. nudicaulis* (L.) Grisebach, *B. antiacantha* Bertoloni, *B. balansae* Mez, *B. chrysantha* Jacquin, *B. karatas* L., *B. hemisphaerica* Lamarck, *B. nidus-puellae* (André) André ex. Mez, *B. pinguin* L., *B. plumieri* (E. Morren) L.B. Smith and *B. trianae* Mez (Rios and Khan, 1998). The most common are known and consumed locally, under names like *cardo* or *banana-do-mato* (bush banana), *piñuelas* (small pineapple) or *karatas*, *gravatá* and *croata* (derived from Amerindian names given to terrestrial bromeliads). Many other bromeliads are cultivated as ornamentals, gathered for fibre extraction or used in traditional medicine (Corrêa, 1952; Purseglove, 1972; Reitz, 1983; Rios and Khan, 1998).

Evolution of pineapple classification

From the first observations of the pineapple by European explorers to the present time, pineapple taxonomy has varied considerably. The first botanical description of cultivated pineapples was by Charles Plumier at the end of the 17th century (but only published in 1755), when he collected plants called *karatas* and *ananas* on the island of Hispaniola. Following the native classification, he created the genus *Bromelia* for the *karatas*, in honour of the Swedish physician Olaf Bromel, and described the *ananas*, using polynomials such as *Ananas aculeatus fructu ovato, carne albida*. In his *Species Plantarum*, Linnaeus (1753) designated the pineapple as *Bromelia ananas* and *Bromelia comosa*, while Miller (1754, 1768) maintained the name *Ananas*, with six varieties, all cultivated. In the following classifications of the 18th and 19th centuries, as pineapple was mainly known from attractive large-fruited types, these varieties and other cultivars were easily confused with species, which resulted in an overwhelming number of different names (Leal *et al*., 1998). Thus, Lindley (1827) used such names as *Ananassa sativa* for ordinary cultivars, *Ananassa lucida* for smooth-leaved cultivars such as 'Smooth Cayenne' (from the variety *Ananas* (*Lucidus*) of the eighth edition of Miller's *Gardener's Dictionary*, published in 1768), *Ananassa debilis* for a particular cultivar with undulated leaves and *Ananassa bracteata* for a crowned pineapple with long bracts. Schultes and Schultes (1830) returned to the original name *Ananas*, with *A. sativus*, *A. debilis*, *A. semiserratus* (instead of *A. lucida*) and *A. bracteatus*. Linden (1879) described a Colombian smooth-leaved cultivar with the 'piping' character under *A. mordilona*. Morren (1878) gave the first clear description of a distinct pineapple, the *yvira*, characterized by long bracts, the absence of a crown and propagation by stolons, which he named *A. macrodontes*. In 1889, both Baker and André described a wild pineapple, with a long scape and a small crowned fruit, respectively, under the names of *Acanthostachys ananassoides* and *A. pancheanus*. In contradiction to this profusion of species descriptions, a few authors, such as Bentham and Hooker (cited by André, 1889), claimed that the genus *Ananas* is monospecific, with multiple wild and cultivated forms. Thus, in his first attempt at simplication, published in the *Flora Brasiliensis*, Mez (1892) recognized only one species, *Ananas sativus*, with five botanical varieties. The variety *lucidus* included the pineapples with smooth leaves and a large fruit, but also the *pitte* or *pitta*, a small-fruited pineapple only cultivated for fibre. *A. debilis* was downgraded to a second variety *debilis*, 'only known from European glasshouses'. The variety *bracteatus* included *A. bracteatus* (Lindl.) Schult. f., but also *A. macrodontes* Morren. The variety *muricatus* was made from *A. muricatus* Schult. f., although Mez expressed doubts about its existence. The last variety, *microstachys*, corresponded to the wild pineapple *Acanthostachys ananassoides* Baker. In 1917, Merrill established the binomial *Ananas comosus*. In 1919, Hassler divided the genus *Ananas* in two sections *Euananas* and *Pseudoananas*. The latter was raised to a distinct monospecific genus by Harms (1930), with *Pseudananas macrodontes* (Morren) Harms. In his second classification, Mez (1934) did not recognize this new genus, and proposed three species: (i) *A. comosus*, including the wild pineapples and the cultivated forms *sativus* (spiny types), *lucidus* (smooth-leaved pineapples) and *debilis* (with doubts); (ii) *A. sagenaria*, corresponding to *A. bracteatus* (Lindl.) Schult. f.; and (iii) *A. macrodontes* Morren. Unfortunately, the second simple classification of Mez was no more successful than the first. From 1934 on, pineapple taxonomy was dominated by the views of L.B. Smith and F. Camargo. These authors divided the genus *Ananas*, renaming and multiplying the species in a long series of publications, without describing new variation (Camargo, 1939, 1943, 1956; Smith, 1939, 1961, 1962; Camargo and Smith, 1968; Smith and Downs, 1979). The resulting overclassification into two genera and nine species (Smith and Downs, 1979; Table 2.1) has been severely criticized on the basis of practicability, as well as inconsistency with avail-

able data on reproductive behaviour and morphological, biochemical and molecular diversity (Leal, 1990; Loison-Cabot, 1992; Leal and Coppens d'Eeckenbrugge, 1996; Coppens d'Eeckenbrugge *et al*., 1997; Leal *et al*., 1998). Indeed, there are no reproductive barriers between the *Ananas* species defined by Smith and Downs and no differences either in their floral structure and cytology or in their chromosome number or breeding system. The studies on diversity of isozymes (García, 1988; Aradhya *et al*., 1994) and on ribosomal and total DNA (Noyer, 1991; Noyer and Lanaud, 1992; Duval *et al*., 1998) all showed a limited differentiation between the different *Ananas* taxa, a strong geographical component of variation and a close affinity between certain wild pineapples and those cultivated for the fruit or for the fibre. The study by Duval *et al*. (1998) justifies the distinction between the generally diploid crowned pineapples propagating by shoots and the tetraploid crownless *yvira* propagating by stolons, although both taxa show much more similarity with each other than with other bromeliads, suggesting that they belong to the same genus.

For these reasons, we return to a much simpler and more consistent classification, taking into account morphological, biochemical and molecular variation, geographical distribution and reproductive biology, according to previous reviews (Leal and Coppens d'Eeckenbrugge, 1996; Leal *et al*., 1998).

Ananas: one genus and two species

In the present classification, all pineapples are regrouped into one *Ananas* genus, characterized among *Bromeliaceae* by the unique feature of their inflorescence, which is fused into a syncarp. The seven valid *Ananas* species proposed by Smith and Downs (1979) are downgraded to the level of five botanical varieties of *A. comosus*.

Ananas *Miller, Gard. Dict. Abr. Ed. 4. 1754*

Synonyms: *Bromelia* L. Spec. Pl. ed. 1 (1753) – *Ananassa* Lindley, Bot. Reg. 13:1081 (1827).
Leaves densely rosulate, blades linear, scarcely enlarged at base, often spiny. Scape evident. Inflorescence densely strobiliform, flowers hermaphrodite, sessile. Sepals free, obtuse, asymmetric, persistent; petals free, erect, violet or purplish pink. Stamens included, pollen ellipsoid, biporate; ovaries coalescing with each other and with the bracts and axis to form a fleshy syncarpic fruit; epigynous tube short; placentae apical; ovules caudate. Fruit succulent.

Table 2.1. Correspondence between the classification of Smith and Downs (1979) and the present classification.

Smith and Downs	Present classification
Pseudananas sagenarius (Arruda da Camara) Camargo Genus *Ananas* Miller including eight species	*Ananas macrodontes* Morren *Ananas comosus* (L.) Merrill including five botanical varieties
Ananas ananassoides (Baker) L.B. Smith *Ananas nanus* (L.B. Smith) L.B. Smith	*Ananas comosus* var. *ananassoides* (Baker) Coppens & Leal
Ananas lucidus Miller	*Ananas comosus* var. *erectifolius* (L.B. Smith) Coppens & Leal
Ananas parguazensis Camargo & L.B. Smith	*Ananas comosus* var. *parguazensis* (Camargo & L.B. Smith) Coppens & Leal
Ananas comosus (L.) Merrill	*Ananas comosus* var. *comosus*
Ananas monstrosus	Invalidated by Leal (1990)
Ananas bracteatus (Lindley) Schultes f. *Ananas fritzmuelleri* Camargo	*Ananas comosus* var. *bracteatus* (Lindl.) Coppens & Leal

Type: *Bromelia ananas* Linnaeus (1753).

KEY TO THE SPECIES AND BOTANICAL VARIETIES

1a. Apical coma inconspicuous or lacking, plant propagating by elongate stolons . . . . . *Ananas macrodontes*

1b. Foliaceous coma usually crowning the syncarp. Plant propagating by the crown and shoots from the stem or peduncle (slips) . . . . . *Ananas comosus*

2a. Flower bracts conspicuous, imbricate and covering the ovary . . . . . *Ananas comosus* var. *bracteatus*

2b. Flower bracts relatively inconspicuous, soon exposing the ovary apices

3a. Spiny leaves. Leaf spines both antrorse and retrorse, blades narrowed towards base . . . . . *Ananas comosus* var. *parguazensis*

3b. Spiny or smooth leaves. Leaf spines all antrorse, blades not narrowed at base

4a. Dense rosette, wide blades, scape wide, fruit medium to large . . . . . *Ananas comosus* var. *comosus*

4b. Sparse rosette, blades usually narrow, scape thin and long, usually erect, fruit small to medium

5a. Blades recurved or erect, spiny. Fruit small to medium . . . . . *Ananas comosus* var. *ananassoides*

5b. Blades erect, usually narrow and unarmed with the exception of the apical thorn. Abundant production of shoots . . . . . *Ananas comosus* var. *erectifolius*

ANANAS MACRODONTES MORREN (Plate 1).

Synonyms: *Ananas microcephalus* (Bak.) Bertoni, An. Cient. Parag. II. 4: 250 (1919) – *Pseudananas macrodontes* (Morren) Harms, Engl. Prantl., Nat. Pflanzenfam. 2. 15a (1930) – *Pseudananas sagenarius* (Arruda da Câmara) Camargo, Rev. Agr. 14. 7–8:15–17 (1939).

Synonymy with *Bromelia sagenaria* Arruda da Câmara and *Bromelia sylvestris* Vellozo is dubious because of very incomplete descriptions, not mentioning clearly the absence of a crown and hence generating a confusion with *A. comosus* var. *bracteatus*.

Local names: *yvira* (Paraguay), *gravatá de rede*, *gravatá de cerca brava*, *nana caçaba* (Brazil). These names, respectively, mean fibre, fishing-net bromeliad, fierce fence bromeliad and strong spine pineapple, in reference to the uses of the plant.

Type: *Ananas macrodontes* E. Morren, Belg. Hortic. 28:140 (1878).

Plant propagating by elongate basal stolons, very rarely by axillary shoots, up to 2 m high. Leaves densely rosulate, generally arching decurved, 2–3 m long, blades 2–7 cm wide, coriaceous, lustrous above, densely lepidote beneath, laxly serrate with curved retrorse and antrorse spines 3–10 mm long. Scape erect, 20–50 cm high, 15–25 mm wide, furfuraceous; scape bracts foliaceous, reduced, red or green. Inflorescence simple, strobilate, globose to ovoid, 8–20 cm long and 6–9 cm wide, 100–200-flowered. Floral bracts densely imbricate, wide at base, lanceolate, acuminate, 2–5 cm long, erect, spiny, red, reddish brown or green, cinereous–lepidote, persistent; flowers opening in upward succession. Sepals erect, asymmetric, ovate to lanceolate, narrowed at base, apiculate, 10–15 mm long, thick with membranous margins, green to red orange, sparsely lepidote; petals tubular–erect, 3–5 cm long, the claw oblong, white, the blade lanceolate, purplish; stamens included, adnate to the petals, shorter than the petals. Syncarp up to about 20 cm long and 10 cm in diameter, not growing appreciably after anthesis, succulent, without leafy crown.

A. macrodontes lacks a crown at the top of the syncarp and reproduces vegetatively by stolons. Exceptional genotypes may also produce shoots directly from the stem (e.g. accession CRF001 at the Venezuelan Centro Nacional de Conservación de Recursos Fitogenéticos) or produce a rudimentary crown (as in specimen US-2622957). Its leaf margins bear strong spines, which are retrorse at the leaf base. The fruits are low in acid. *A. macrodontes* has been reported as self-compatible, with $2n = 4x = 100$ chromosomes (Collins, 1960). Its natural distribution corresponds to coastal and southern Brazil, up to Pernambuco, and to the drainage of the Paraguay and Paraná rivers, from south-eastern Paraguay and north-eastern Argentina up to Mato Grosso (Coppens d'Eeckenbrugge *et al.*, 1997). Its habitat is limited to forest areas, under semidense

shade. It is subjected to a rainy season during most of the year or even to periods of flooding. Populations of *A. macrodontes* are rare now because of a very strong reduction of its habitat.

Camargo (cited by Reyes-Zumeta, 1967) considered that this species includes at least three botanical varieties, one corresponding to the description by Morren and another to *A. microcephalus*, described by Bertoni (1919) in Paraguay. On the contrary, Baker and Collins observed very little variation in those areas (Smith, 1939). However, the few types observed by Ferreira *et al.* (1992) in Paraguay and South Brazil showed significant variation, which was confirmed by the restriction fragment length polymorphism (RFLP) study of Duval *et al.* (1998).

ANANAS COMOSUS (LINNAEUS) MERRILL.
Synonyms: *Bromelia ananas* L., Sp. Pl. 285 (1753) – *Bromelia comosa* L., Herb. Amboin. (1754), based on *Anassa domestica* Rumphius – *Ananas sativus sensu* Mez, Mart. Fl. Bras. 3(3):290 (1892), in part – *Ananas comosus* (L.) Merril *sensu* Mez, *Pflanzenreich* IV. 32:102 (1934) – see also synonyms in the following descriptions.
Common names: *nanas* or *ananas* (in many Indian languages of South America, and in French and Portuguese), *piña* (Spanish), pineapple.
Type: *Anassa domestica* Rumphius from Amboina in the Moluccas, Belg. Hortic. 28:140 (1878).

Plant not producing stolons but axillary shoots from the stem and/or slips from the scape, up to 1.8 m high. Leaves densely rosulate, scarcely enlarged at base, coriaceous, densely lepidote beneath. Scape evident, erect; scape bracts foliaceous, usually reddish at base. Inflorescence densely strobiliform, usually crowned with one or several rosettes of foliaceous bracts; flowers sessile, highly variable in number, from less than 50 to more than 150. Floral bracts broadly elliptic to lanceolate, acuminate, sublepidote or lepidote. Sepals free, obtuse, slightly asymmetric; petals free, erect, violet or purplish pink, stamens included, pollen biporate and ellipsoid; ovaries coalescing with each other and with the bracts and axis to form a fleshy compound fruit; epigynous tube short; placentae apical; ovules caudate.

Instead of producing stolons, *A. comosus* multiplies by stem shoots (terrestrial and aerial), slips (from the peduncle) and crown. The syncarpic fruit is formed of 50–200 berries. The spines are generally antrorse but some genotypes also exhibit a few retrorse spines. As commonly found in *Bromeliaceae*, *A. comosus* is diploid, with 50 minute and almost spherical chromosomes (Collins and Kerns, 1931; Canpinpin and Rotor, 1937; Marchant, 1967; Sharma and Ghosh, 1971; Lin *et al.*, 1987; Brown and Gilmartin, 1989; Dujardin, 1991). Giant unreduced gametes may appear and produce natural triploids and tetraploids (Collins, 1933, 1960). Most genotypes present reduced self-fertility because of the action of a self-incompatibility system, with considerable variation in its expression (Coppens d'Eeckenbrugge *et al.*, 1993). The natural distribution of *A. comosus* corresponds to that of its variety *ananassoides*, extending east of the Andes (with some presence in the foothills of the central Andes of Colombia), from northern South America to northern Argentina and Paraguay.

Ananas comosus *var.* ananassoides *(Baker) Coppens & Leal (Plate 2).* Synonyms: *Acantostachys ananassoides* Baker, Handb. Brom. 25 (1889) – *Ananas microstachys* Lindman, Sv. Vet-akad. Handl. III. 24(8):39 (1891; *nom. Ill.*) – *Ananas sativus* var. *microstachys* (Lindm.) Mez, Mart. Fl. Bras. 3(3):294 (1892) – *Ananas guaraniticus* Bertoni, An. Cient. Parag. II. 4: 274 (1919) – *Ananas comosus* var. *microstachys* (Mez) L.B. Smith, Contr. Gray Herb. 104:72 (1934) – *Ananas ananassoides* (Baker) L.B. Smith, Bot. Mus. Leafl. Harvard 7:70 (1939) – *Ananas nanus* (L.B. Smith) L.B. Smith, Brom. Soc. Bull. 12:54 (1962) – *Ananas ginesio-linsii* Reitz, Brom. Soc. Bull. 18:109 (1968).
Local names: *ananaí* or *nanaí*, *ananas de ramosa* (Brazil, Pará), *curibijul*, *maya piñon*, *piñuela*, *ananas do indio*.
Lectotype: Regnell III 1261 in part (holotype, P), Caldas, Minas Gerais.

Leaves up to 2 m long and narrow; blades linear, usually less than 4 cm wide,

subdensely serrate with wholly antrorse spines. Scape elongate, slender, usually less than 15 mm thick; scape bracts large, subfoliaceous. Inflorescence small to medium, globose to cylindrical. Fruit slightly enlarged after anthesis, flesh scant to abundant, fibrous; coma relatively large at maturity.

Ananas nanus (L.B. Smith) L.B. Smith is considered here just a dwarf form of *A. comosus* var. *ananassoides*. The constancy of the distinctions reported by Smith (1962) do not constitute any argument in a vegetatively propagated plant. Indeed, sexual hybrids segregate for size and most other traits. *Ananas ginesio-linsii* Reitz (*ananas do indio*) is a triploid clone showing particular vegetative vigour (Lin *et al*., 1987; Dujardin, 1991).

A. comosus var. *ananassoides* is the most common wild pineapple and the botanical variety that shows the highest genetic diversity; it is very probably at the origin of the cultivated pineapples (Leal and Coppens d'Eeckenbrugge, 1996; Coppens d'Eeckenbrugge *et al*., 1997; Duval *et al*., 1998). *A. comosus* var. *ananassoides* is found in all tropical areas of South America east of the Andes, generally in savannahs or in low-shaded forest, growing well on soils with limited water-holding capacity (sand, rocks) and forming populations of very variable densities. However, a few genotypes thrive in dense rain forest (in the Guianas). Most populations are monoclonal, but some are polyclonal, with variation of recent sexual origin (Duval *et al*., 1997). The plant has long and generally narrow spiny leaves and bears a small to medium, globular to cylindrical syncarp on a long and thin peduncle. The fruit is often seedy, and its pulp is white or yellow, firm and fibrous, palatable, with a high sugar and acidity content. Some clones producing a fruit of intermediate size (as compared with the *comosus* variety) are found both wild and cultivated in the Guianas. Some dwarf types have been recently cultivated intensively as ornamentals.

Ananas comosus *var.* erectifolius *(L.B. Smith) Coppens & Leal (Plate 3).* Synonyms: *Ananas sativus* var. *Duckei* Camargo, Rev. Agr. 14. 7–8:13–14 (1939), without Latin diagnosis – *Ananas erectifolius* L.B. Smith, Bot. Mus. Leafl. Harvard 7:78 (1939) – *Ananas lucidus* Miller, *sensu* Smith, Bromel. In: *Flora de Venezuela* 12(1):1–361 (1971).
Synonymy with the *lucidus* variety of Miller (Gard. Dict. ed. 8) is not founded because the latter was created for the smooth-leaved cultivars giving a large fruit.
Common names: *curagua*, *curauá*, *curaná*, *kulaiwat*, *pitte*.

Leaves stiff and erect, 1 m or longer, blades about 35 mm wide, entire or nearly so, except for the pungent apex. Scape erect, elongate, slender, to 15 mm thick; scape bracts foliaceous, erect. Syncarp small, cylindrical or subcylindrical; floral bracts small, entire. Fruit slightly larger than inflorescence, coma relatively large, sometimes surrounded by additional crownlets; flesh scant, fibrous, unpalatable.

Ananas comosus var. *erectifolius* is essentially distinguished from *A. comosus* var. *ananassoides* by its smooth leaves. It is cultivated by the natives in the Guianas, including the Orinoco basin, and in the north of the Amazon basin, for its very strong and long fibres, used to make hammocks and fishing nets (Leal and Amaya, 1991). The dry fibres constitute 6% of the plant weight (Camargo, 1943). *A. comosus* var. *erectifolius* has never been found in the wild. Plants are medium-sized, with abundant shoots and numerous erect leaves and with a small, very fibrous (inedible) fruit. It is also discriminated from *A. comosus* var. *ananassoides* by the absence of spines along the leaf margin. However, spiny types have been observed under cultivation or as mutants in germplasm collections. The absence of spines, as well as its erect habit, are probably the product of human selection for high yield of easily extractable fibres from strains of *A. comosus* var. *ananassoides*. According to the DNA diversity study of Duval *et al*. (1998), different clones of *A. comosus* var. *erectifolius* show more affinity with different clones of *A. comosus* var. *ananassoides* than with each other, which suggests that this process may have taken place independently at different times or places, or both.

Ananas comosus *var.* parguazensis *(Camargo & L.B. Smith) Coppens & Leal (Plate 4).* Synonyms: *Ananas ananassoides sensu* L.B.

Smith in part, Contr. U.S. Natl. Herb. 33:300 (1957) as to Colombian material; Fl. Venez. 12:341 (1971) as to Venezuelan material – *Ananas parguazensis* Camargo & L.B. Smith, Phytol. 16:464 (1968).
Common names: *piña montañera* (Amazonas, Venezuela), *ananaí* (Roraima, Brazil), *kurupira-nana* (Río Negro, Brazil), *gravatá* (Pará, Brazil).
Type: Camargo 3 (holotype, COL; isotype, US), Angelita, Bolívar, Venezuela, 16 June 1966.

Leaves up to 2 m long, blades wide (usually more than 3 cm), somewhat contracted towards base, green to red, sinuate–serrate, spines strong, antrorse and retrorse. Scape slender, elongate, often decumbent (depending on fruit size); scape bracts foliaceous, notably dilated above base. Inflorescence few-flowered, subglobose, 4–10 cm long in fruit; apical coma large (reaching 30 cm in height), basally more or less retrorse serrate. Fruit succulent, flesh palatable.

As mentioned by Smith and Downs (1979), *Ananas pancheanus* André could also correspond to *A. comosus* var. *parguazensis*. Indeed, André (1889) mentions a forest habitat, wide leaves (6 cm), antrorse and retrorse spines and a small subspherical syncarp. On the other hand, the short and thin spines, with a density increasing regularly from the base to the top of the leaf, are not typical of the variety. The exsiccata observed in Kew is too poor to offer an opinion on.

The wild *A. comosus* var. *parguazensis* is very similar to *A. comosus* var. *ananassoides*, with a difference in the retrorse orientation of some spines and a wider leaf slightly constricted at its base. Its distribution is mostly limited to the Orinoco and Rio Negro basins, with a few observations in eastern Colombia and in the north-eastern Amazon (Coppens d'Eeckenbrugge *et al*., 1997) and it shows less variability than *A. comosus* var. *ananassoides* (Duval *et al*., 1998). While *A. comosus* var. *ananassoides* shows a higher water-use efficiency and grows in both partial shade and full sun, *A. comosus* var. *parguazensis* is restricted to shadier environments (Leal and Medina, 1995). It grows in the lowland forests, under canopies of variable densities, from clearings or river-banks to dense forest.

Ananas comosus *var.* comosus *(Plate 5).*
Synonyms (not mentioning horticultural forms described as cultivars): *Bromelia ananas* L., Sp. Pl. 285 (1753) – *Bromelia comosa* L., Herb. Amboin. (1754), based on *Anassa domestica* Rumphius – *Ananas* varieties described by Miller, Gard. Dict. ed. 8 (1768) – *Ananassa sativa* Lindley, *Ananassa lucida* Lindley and *Ananassa debilis* Lindley, Bot. Reg. 13:1068 (1827) – *Ananas sativus* Schultes f., *Ananas debilis* Schultes f. and *Ananas semiserratus* Schultes f., in Roemer & Schultes, Syst. 7(2):1283, 1287 (1830) – *Ananas sativus* var. *lucidus* Baker, Handb. Brom., 23 (1889) – *Ananas mordilona* Linden, Belg. Hort. 29, 302 (1889) – *Ananas sativus* var. *lucidus* Mill. and *Ananas sativus* var. *debilis* Lindley, Mez, Mart. Fl. Bras. 3(3):292–293 (1892) – *Ananas sativus* var. *pyramidalis* (Miller) Bertoni, *Ananas sativus* var. *viridis* (Miller) Bertoni and *Ananas sativus* var. *hispanorum* Bertoni, An. Cient. Parag. II. 4: 271, 272 (1919) – *Ananas comosus* f. *sativus* (Lindl.) Mez, *Ananas comosus* f. *lucidus* (Mill.) Mez and *Ananas comosus* f. *debilis* (Lindl.) Mez, *Pflanzenreich* IV. 32:102–104 (1934) – *Ananas comosus* (L.) Merril, interpr. Rumph. Herb. Amb.
Common names: *ananas*, *nanas*, *piña*, pineapple, *abacaxi* (Brazil), *matzatli* (Aztec).

Leaves numerous and wide, spines antrorse if present. Scape stout, usually 2 cm or more in width and less than 40 cm in length. Inflorescence large, many-flowered. Floral bracts inconspicuous, soon exposing the apices of the ovaries, weakly serrulate or entire. Syncarp growing appreciably after anthesis, to reach a final size several times superior to that of the inflorescence; fruit fleshy; seeds usually rare.

The highly variable *A. comosus* var. *comosus* is characterized by its large fruit (up to several kilograms in some cultivars), borne on a wide and strong peduncle. Its leaves are numerous (40–80) and wide (> 5 cm). In spiny cultivars, spines are antrorse and generally denser than in other botanical varieties. Certain cultivars are partially spiny (e.g. the cultivar 'Smooth Cayenne') or even completely smooth (as in the cultivars with the 'piping' trait). Seeds are rare because most cultivars present reduced fertility combined with self-incompatibility (Coppens

d'Eeckenbrugge *et al*., 1993). Since the first Spanish and Portuguese great voyages, cultivation of *A. comosus* var. *comosus* has become pantropical.

The species *A. monstrosus* (Carrière) L.B. Smith was invalidated by Leal (1990) because the crownless fruit characteristic is not stable. In addition, the names *A. monstrosus* and *A. lyman-smithii* Camargo, on which it is based, are illegitimate, the former because Carrière never intended to describe a new species and the latter because it is a *nomen nudum*.

Ananas comosus *var.* bracteatus *(Lindl.) Coppens & Leal (Plate 6).* Synonyms: *Ananassa bracteata* Lindley, Bot. Reg. 13:1081 (1827) – *Ananas bracteatus* (Lindley) Schultes f., Syst. 7(2) (1830) – *Ananas sativus* var. *bracteatus* (Lindley) Mez, Mart. Fl. Bras. 3(3):293 (1892) – *Ananas sagenaria sensu* Mez, *Pflanzenreich* IV. 32:104 (1934) – *Ananas bracteatus* var. *albus* L.B. Smith, Bot. Mus. Leafl. Harvard 7:76 (1939) – *Ananas fritzmuelleri* Camargo, Bol. Téc. Inst. Agr. Norte, Pará. 1:16 (1943).
As mentioned in the description of *A. macrodontes* Morren, there is a possible synonymy with *Bromelia sagenaria* Arruda da Câmara and *Bromelia sylvestris* Vellozo (and all subsequent names referring to these two descriptions).
Common names: *ananas de cerca*, *ananas bravo*, *ananas do mato*, *karaguata-ruha* (southern Brazil).
Type: Lyndley s n (holotype, CGE n v), or original description and plate.

Leaf blades wide, coarsely and usually laxly spinose–serrate, spines antrorse or antrorse and retrorse. Scape thick and stout. Syncarp medium to large. Floral bracts conspicuous, imbricate and covering the ovaries, coarsely serrate, usually red or pink. Fruit succulent at maturity.

A. comosus var. *bracteatus* has the same original southern distribution area as *A. macrodontes*. It is always found cultivated as a living hedge, for fibre and fruit juice, or abandoned in ancient settlements (Baker and Collins, 1939; Duval *et al*., 1997). The plant is very vigorous, with wide and long leaves, large spines and abundant production of shoots. The inflorescence is characterized by its long bracts (longer than the fruitlet) of a bright pink to red colour. The fruit and peduncle are medium-sized. There are two main forms of *A. comosus* var. *bracteatus*. The most common corresponds to *A. bracteatus sensu* Smith & Downs, with a spectacular bright red inflorescence and antrorse spines, of which a variegated cultivar has been derived and propagated in all the tropical regions as a garden ornamental. It has also been used for the cut-flower market and a further mutation suppressing spines has been selected recently. The second form corresponds to *A. fritzmuelleri* Camargo, with antrorse and retrorse spines. Both forms show very little variation, suggesting that they are very particular types, probably selected by humans and dispersed through clonal propagation and still capable of developing subspontaneous populations. They share certain morphological, biochemical and DNA characters with *A. macrodontes*. In diversity studies, they appear uniform and well grouped (García, 1988; Duval and Coppens d'Eeckenbrugge, 1993; Aradhya *et al*., 1994; Duval *et al*., 1998), at some distance from the other botanical varieties of *A. comosus*, but closer to *A. comosus* than to *A. macrodontes* (Duval *et al*., 1998). *A. comosus* var. *bracteatus* hybridizes easily with *A. comosus*.

Origin and Evolution

After inventorying and describing the variability found in Paraguay, Bertoni (1919) stated that the pineapple was domesticated by the Tupi-Guarani Indians from *A. guaraniticus* (*A. comosus* var. *ananassoides*) and then accompanied them in their northward migrations to the Antilles, northern Andes and Central America. This hypothesis has been retained in many reviews on crop origins (e.g. Collins, 1948, 1949, 1960, Purseglove, 1972; Pickersgill, 1976; Sauer, 1993). In his discussion of Vavilov's theory, Brücher (1971) underlined the presence of wild forms and primitive cultivars in the north of South America and proposed that domestication occurred on the Guiana shield, along the river system, and, possibly,

in north-eastern Brazil. This work, written in German and presenting imperfect information on pineapple taxonomy and distribution, was largely ignored.

The hypothesis of a northern origin of pineapple came back with Leal and Antoni in 1981. These authors suggested that the centre of origin of the genus should be located in an area within 10°N–10°S latitude and 55°–75°W longitude, because the flora of this region is endemic and included the largest number of species considered valid at that time. They proposed that south-eastern Brazil could be a secondary centre of origin and distribution. Extensive expeditions in Venezuela, Brazil and French Guiana (Leal *et al.*, 1986; Ferreira *et al.*, 1992; Duval *et al.*, 1997) widened significantly the known diversity of wild and cultivated forms and reinforced the hypothesis of a northern centre of origin for the cultivated pineapple. Indeed, a wider morphological variation was observed both in the wild and under cultivation in the areas to the north of the Amazon River (Orinoco and Rio Negro basins, Amapá, Guianas) than in the southern areas (Paraguay, south of Brazil).

Four botanical varieties of *A. comosus* occur in the area north of the Amazon River: the cultivated *A. comosus* var. *comosus*, with many cultivars, and *A. comosus* var. *erectifolius*, and the wild *A. comosus* var. *parguazensis* and *A. comosus* var. *ananassoides*, with a wide range of morphological and adaptive variation, from forest types to dry savannah types, including medium-fruited types still submitted to domestication cycles. In the southern areas are found *A. macrodontes* and representatives of three botanical varieties of *A. comosus*: the cultivated *A. comosus* var. *comosus* and *A. comosus* var. *bracteatus* (the latter with poor morphological variation) and savannah types of *A. comosus* var. *ananassoides* (Leal and Coppens d'Eeckenbrugge, 1996; Coppens d'Eeckenbrugge *et al.*, 1997; Duval *et al.*, 1997). Molecular studies tend to confirm this hypothesis (Duval *et al.*, 1998). Thus, it seems that *A. comosus* var. *comosus* and *A. comosus* var. *erectifolius* evolved from *A. comosus* var. *ananassoides* and/or *A. comosus* var. *parguazensis*, the first by a selection based on large fruit size, through an increase in the fruitlet number and size, high quality (lower acidity) and reduced seediness, and the second by a selection for long, fibrous and smooth leaves. Other traits were necessarily modified in the course of domestication and selection.

Increased fruit size in *A. comosus* var. *comosus* implied increased size of other organs, i.e. wider leaves, bigger stem, shorter and wider peduncle. Sensitivity to natural flowering induction was reduced, allowing a longer cycle and hence a larger fruit. Cultivation based on asexual propagation and artificial selection of seedless genotypes reduced the natural selective pressure on fertility and reinforced self-incompatibility. Domestication also influenced spininess. In some cases, spininess was suppressed by the selection of rare dominant mutations. The excellence of the selections obtained by the Amerindians, still unsurpassed, their knowledge of the crop and the wide pre-Columbian distribution of the pineapple all indicate a very ancient domestication, probably several thousands of years before Christ.

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3 Breeding and Variety Improvement

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The pineapple industry of the world is dominated by the cultivar 'Smooth Cayenne', which is used both for fresh fruit and for processing. The near-total reliance on a single cultivar in crop cultivation is uncommon and is made even more unbelievable by the fact that 'Smooth Cayenne' has been the backbone of the global pineapple industry for more than a century. First collected by Perrotet in 1819 in French Guiana under its local name 'Maipuri' (Perrotet, 1825), it rapidly spread to other geographical regions, has adapted well and is known by such other synonyms as 'Kew', 'Giant Kew', 'Champaka' and 'Sarawak'. The 'Smooth Cayenne' monopoly is undoubtedly due to its high yield, adaptability and good characteristics for canning. Further, highly specialized systems of production and processing protocols have been developed almost exclusively for this cultivar. These factors, together with impending high costs and attendant inconveniences in changing to a new variety, account for the difficulty in replacing 'Smooth Cayenne'.

Global Pineapple Breeding Research

The overdependence of the pineapple industry on a single cultivar with a narrow genetic base has made it extremely vulnerable to the threats of pests and diseases. Development of new, resistant cultivars seemed the right strategy to redress this situation. Further, while 'Smooth Cayenne' is quite good for processing, the fresh-pineapple markets in the world are more diversified and, where a choice is offered, this cultivar is not always preferred. These are primary justifications for the commencement of breeding programmes for pineapple worldwide.

In 1914, the Pineapple Growers Association of Hawaii started one of the earliest and most concerted efforts in pineapple improvement. The experimental station of this association later became the Pineapple Research Institute of Hawaii (PRI). The works of K.R. Kerns and J.L. Collins from the PRI are renowned and are still often cited by present-day researchers. One of the main objectives of the PRI programmes was to develop pest and disease resistance in a 'Smooth Cayenne'-type variety. Varieties were developed which had better resistance to *Phytophthora*, mealybug wilt, nematodes, pink disease and internal brown spot. Some selections also had higher vitamins A and C, less acid in winter-ripened fruits, a better harvesting peak, higher yield and plant vigour and improved cannery recovery. Many varieties were selected which were better than 'Smooth Cayenne' in certain individual characteristics, but eventually none could replace 'Smooth Cayenne' because, after extensive evaluation, each would reveal a fatal flaw

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(Williams and Fleisch, 1993). The PRI closed in 1975 and evaluation of progenies was completed at the Maui Pineapple Company in 1985. A small number of the PRI varieties and the genetic collection were turned over to the US Department of Agriculture (USDA) germplasm repository in 1986.

Many other pineapple-growing countries have also started breeding programmes to develop high-yielding varieties with specific adaptation to their own environments. Most current breeding programmes are focused on the development of cultivars for the fresh market. It is important to note that hybridization programmes attempting to replace 'Smooth Cayenne' for processing have been rare since the termination of the PRI programme in Hawaii. Most hybridization programmes revolve around the 'Smooth Cayenne' because of its all-round good qualities and universal acceptance. In 1926, Taiwan (then Formosa) started a breeding programme using 'Smooth Cayenne' crossed with several of its local varieties, 'Ohi', 'Uhi', 'Anpi' and 'Seihi'. A later hybridization programme using 'Smooth Cayenne' and 'Queen' resulted in the selection of 'Tainung 4' ('Easy Peeler'), the eyes (fruitlets) of which can be picked off for eating without having to peel the fruit (Fitchet, 1989). This programme continued, with the release of 'Tainung 13' and 'Tainung 16' in 1995 and 1996, respectively (Chang *et al*., 1997).

In Malaysia, early pineapple improvement programmes focused on the selection of promising variants in clonal fields. This has resulted in the development of 'Masmerah', a higher-yielding variant of the 'Singapore Spanish' (Wee, 1974). Later hybridization programmes conducted by the Malaysian Agricultural Research and Development Institute (MARDI) developed a hybrid called 'Nanas Johor' from a cross between 'Smooth Cayenne' and 'Singapore Spanish' (Chan and Lee, 1985). In 1996, another hybrid called 'Josapine' suitable for table fruit, was developed from a cross between 'Nanas Johor' and 'Sarawak' (a variant of 'Smooth Cayenne') (Chan and Lee, 1996).

The 'Smooth Cayenne' was again featured in breeding programmes carried out in the Philippines, Côte d'Ivoire, Cuba, Puerto Rico and Australia. In the Philippines, the recent breeding programme carried out by the Institute of Plant Breeding (Los Baños) was based on crosses between 'Smooth Cayenne' and 'Queen', with the objective of developing spineless 'Queen' types. One selection was micropropagated (Villegas *et al*., 1995). The research on pineapple in Côte d'Ivoire was started in 1978 and conducted by the fruit department (Département des Productions Fruitières et Horticoles) of the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD-FLHOR). 'Smooth Cayenne' was crossed with 'Perolera' (in fact 'Manzana') with the objectives of developing high ascorbic acid content for resistance to black-heart disorder (an internal fruit breakdown), developing resistance to *Phytophthora* and nematodes and prevention of green ripe fruits (internal flesh colour turns yellow before the change of peel colour) (Loison-Cabot, 1987). A new hybrid called 'Scarlett', with commercial potential as a fresh fruit, was selected from this hybridization programme (Coppens d'Eeckenbrugge and Marie, 2000).

In Cuba, the hybridization programme was started in 1991 using 'Serrana' ('Smooth Cayenne') × 'Perolera' and three hybrids were micropropagated for commercial fruit production (Benega *et al*., 1998b). In Puerto Rico, a natural cross between 'Smooth Cayenne' and 'Española Roja' resulted in a selection called PR1–67 (Ramírez *et al*., 1972). In Australia, the breeding programme utilizes mainly 'Smooth Cayenne', 'Queen' and selected PRI hybrids. Sanewski (1998) found that the PRI hybrids '73–50', '53–116' and '59–656' and the Philippine hybrid '24–80' generally produced more hybrid progenies with commercially acceptable attributes for the fresh-fruit market.

In Brazil, the major cultivars are 'Pérola' and 'Smooth Cayenne' and the main objective of the breeding programme conducted by the Empresa Brasileira de Pesquisa Agropecuaria (EMBRAPA) was to develop cultivars with resistance to fusariosis disease caused by *Fusarium subglutinans*. The resistant parents used in the crosses with 'Pérola' and 'Smooth Cayenne' gave the highest pro-

portion of hybrid progenies with desirable characters (Cabral *et al*., 1993). Fifty-seven hybrids have been selected for further evaluation. Three 'Perolera' × 'Smooth Cayenne' and two 'Primavera' × 'Smooth Cayenne' hybrids are being tested for eventual release.

Breeding strategies used by most countries appeared to be hybridization and selection of the segregating hybrid progenies. It was evident that 'Smooth Cayenne', the standard benchmark cultivar worldwide, is the favourite parent for the crosses. It seemed fairly strange that hitherto, only a handful of hybrids have been released from these hybridization programmes. As noted by Nakasone (1976): 'breeding work has been done in Hawaii, Australia, Taiwan, Malaysia, South Africa and other areas, resulting in significant contributions to knowledge in cytology and genetics, but not to the list of new cultivars'. This strongly emphasizes the quality and stability in performance of the singular cultivar 'Smooth Cayenne', whose durability and ability to weather the advent of new hybrids are really remarkable.

Germplasm Resources

Origin, diversity and description of cultivars

Early European pineapple experts recognized as many as 48–68 pineapple cultivars and classified them on the basis of spininess, fruit shape and flower colour (Munro, 1835; Beer, 1857). Most of them originated from coastal regions, such as the Caribbean, from which sea trade favoured their distribution to other tropical countries and to the European glasshouses. Others were grown from seeds in Europe. Nearly all disappeared with European production and only 'Queen', 'Smooth Cayenne', 'Baronne de Rothschild', 'Havannah' ('Española Roja'), 'Black Antigua' and 'Montserrat' are still known today. The first two have reached all tropical and subtropical countries. 'Singapore Spanish', which was introduced very early, is still cultivated to some extent in Asia. Other cultivars are economically important in their region of origin, such as 'Pérola' in Brazil, 'Española Roja' in the Caribbean and 'Perolera' and 'Manzana' in the Andes of Colombia and Venezuela. Germplasm movement has been accompanied by clonal differentiation and/or selection and the cultivars have frequently been renamed, often with the same or similar names (e.g. 'Sugar Loaf'). Some authors have classified them into horticultural groups. The last of these classifications, by Py *et al.* (1987), recognizes five such groups: 'Cayenne', 'Queen', 'Spanish', 'Pernambuco' and 'Perolera'. Since then, a much wider diversity of cultivars has been collected and characterized, making the earlier classifications inadequate, confusing and inappropriate. Coppens d'Eeckenbrugge *et al.* (1997) proposed abandoning such classifications and coming back to the international nomenclature for cultivars (Anon., 1980). Accordingly, a new name can only be attributed to a new cultivar whose characteristics are stable and clearly distinct, regardless of whether the method of development is through clonal selection or sexual recombination. Thus, most minor variants and clonal selections should not be considered as new cultivars, although a small difference in fruit size may be economically very significant. To take into account interclonal genetic variation and regional nomenclature, Coppens d'Eeckenbrugge *et al.* (1997) proposed mentioning local names or specific clones together with the cultivar name, which would give, for instance, 'Champaka' ('Smooth Cayenne') and 'McGregor' ('Queen').

Main cultivars

'Smooth Cayenne' (Plate 7), or 'Cayenne Lisse', is still common in the Guianas under the name 'Maipuri', meaning 'tapir'. It has been renamed 'Kew', 'Sarawak', 'Esmeralda', 'Claire', 'Typhoon' and 'Saint Michel'. The ovoid medium-sized fruit (1.5–2.5 kg) of 'Smooth Cayenne' is held on a short and strong peduncle (Fig. 3.1). It ripens progressively, turning yellow from the base to the top, which is reflected in a strong internal maturity gradient too. The flesh is pale yellow, soft and juicy, with considerable

variation in sugar (from 13 to 19°Brix) and acidity, depending on environmental conditions – mainly rain and temperature – and low ascorbic acid content. Despite the high sugar content of 'Smooth Cayenne', its acidity is often considered excessive among tropical consumers and this has largely contributed to the image of pineapple as an acidic fruit. 'Smooth Cayenne' juice is not of good quality, because of poor colour, high sugar and turbidity. The plant is medium-sized (80–100 cm), with 60–80 dark green leaves (*c*. 100 cm long and 6 cm wide), which bear small spines at their base and tip. Vegetative propagation is normally by shoots and slips, which are quite limited in production. The production cycle of 'Smooth Cayenne' is longer than that of most other cultivars and this is exacerbated in cool climates. 'Smooth Cayenne' is sensitive to many known pests (fruit borers, mites, symphillids, nematodes) and diseases (mealybug wilt, fusariosis, fruitlet core rot, butt rot) and to internal browning (Rohrbach and Schmitt, 1994; Bello *et al*., 1997a,b). However, it is considered to be tolerant to *Phytophthora* sp. (Py *et al*., 1987) and resistant to fruit collapse caused by *Erwinia chrysanthemi* Burkbolder (Lim and Lowings, 1979).

Fig. 3.1. 'Smooth Cayenne'.

The cultivar 'Cayenne Baronne de Rothschild', cultivated in West Africa, is the spiny form of 'Smooth Cayenne'. 'Hilo', a Hawaiian variant, might merit cultivar status as it produces many more slips than the standard 'Smooth Cayenne' (Collins, 1960). Collins and Kerns (1938) and Collins (1960) have described more than 30 'Smooth Cayenne' mutants in Hawaii, the most common being spiny leaves, multiple crowns and fasciated crowns or fruits and collar of slips. The most interesting are 'seedy fruit', a series of mutations that breaks down self-incompatibility in pollen, and resistance to mealybug wilt, which was also observed in Mexico (Torres Navarro *et al*., 1989).

'Singapore Spanish' (Plate 8) is second in importance for canning. Other names and particular strains are 'Singapore Canning', 'Ruby', 'Red Pine', 'Nanas Merah', 'Nangka', 'Gandul', 'Betek' and 'Masmerah' (Wee, 1972). 'Singapore Spanish' is cultivated in South Asia, particularly in Malaysia, because of its good adaptation to peat soils and its golden-yellow flesh colour. Fruits are small (around 1 kg – heavier in 'Masmerah'), cylindrical and dark purple, turning copper-orange when ripening (Fig. 3.2). Sugar and acidity are low (10–12°Brix) and the taste is poor; however, the juice is of good colour and quality. The plant is medium-sized (80–100 cm), with 35–70 dark green leaves, about 150 cm long and 5 cm wide. Leaf spininess is highly variable from clone to clone, from complete spininess to very few spines. The bracts of the peduncle and inflorescence are bright red. The plant is vigorous and produces many slips (about two to six) and shoots. Multiple crowns are frequent. 'Singapore Spanish' is adapted to high soil pH, which is probably related to its tolerance to *Phytophthora*, a fungus that develops better in such conditions. It shows severe chlorosis when exposed to high manganese concentration in the soil. It is also sensitive to fruit collapse, the most serious disease in Malaysia (Lim and Lowings, 1979), and to nematodes (Collins and Hagan, 1932).

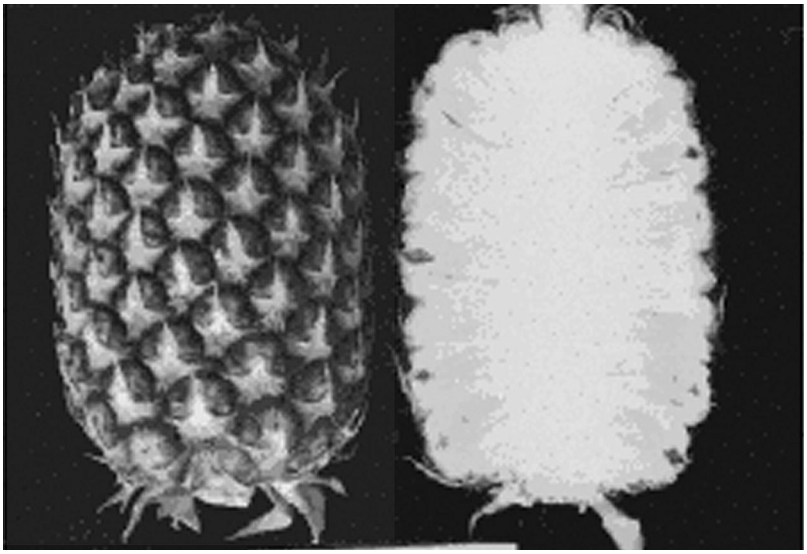

Fig. 3.2. 'Gandul' (cv. 'Singapore Spanish').

The cultivar 'Selangor Green', also named 'Green Pine', 'Green Spanish', 'Nanas Hijau' and 'Selassie', is derived from a mutation suppressing anthocyanins in all the organs of 'Singapore Spanish'. Thus the leaves and inflorescence are uniformly green, the petals pale yellow and the fruit yellow at maturity. Other traits have not been altered. Another mutation produced a variegated red-fruited cultivar used as an ornamental.

The cultivar 'Queen' (Plate 9) is widely distributed, but it is more particularly cultivated in the southern hemisphere, in South Africa and Australia, for the fresh-fruit market. It has been called 'Mauritius', 'Malacca', 'Red Ceylon', 'Buitenzorg', 'Victoria', 'Ripley Queen' and 'Alexandra' (Mendiola *et al*., 1951; Leal, 1990). In Malaysia, it is called 'Moris' and Chan and Lee (1995) have described several variants. 'McGregor' is a vigorous Australian selection. The tetraploid 'Z' or 'James Queen' was found in South Africa (Nyenhuis, 1974). The plant is small (60–80 cm), with short and very spiny silvery leaves, and gives a small fruit (0.5–1 kg), with a full yellow shell and small prominent eyes (Fig. 3.3). The golden-yellow pulp is crispy and sweet (14–18°Brix), with an excellent flavour and long shelf-life. The production of slips and shoots varies widely between clones. 'Queen' is a robust cultivar, showing more general tolerance to stress, pests and diseases than 'Smooth Cayenne'. On the other hand, it is susceptible to *Phytophthora* and fruit collapse and highly susceptible to chilling and internal browning, particularly if harvested before maturity, and to fruitlet core rot and butt rot (Lim, 1971; Winks *et al*., 1985; Swarts, 1990; Lutchmeah, 1992).

'Española Roja' or 'Red Spanish' (Plate 10) is widely cultivated in Venezuela and the Caribbean basin, under names such as 'Black Spanish', 'Key Largo', Havannah' or 'Habana', 'Cubana', 'Cowboy', 'Bull Head', 'Cumanesa' and 'Native Philippine Red' (Leal, 1990). The fruit is medium-sized (1.2–2 kg) and orange, with a barrel shape. The flesh is firm, pale, aromatic and sweet, with moderate sugar content (around 12°Brix) but low acidity. The plant is medium-sized, with spiny or half-spiny dark green leaves. Smooth clones have been selected. Floral bracts are an intense bright red colour. The plant regularly produces some slips (about one to three) and suckers. 'Española Roja' is vigorous and tolerant to high temperature, drought, internal browning, butt rot, wilt and *Phytophthora* (Py *et al*., 1987; Rohrbach and Schmitt, 1994), but not to high

Fig. 3.3. 'Mauritius' (cv. 'Queen').

manganese in the soil and nematodes (Ayala *et al.*, 1969). It is highly susceptible to the South American lepidopter *Strymon basilides* (Geyer).

'Pérola' (Plate 11), 'Pernambuco' or 'Branco de Pernambuco' is the main cultivar in the Brazilian fresh market. 'Jupi' is a particular strain. In Florida, it has also been named 'Abacaxi', 'Abakka' and 'Eleuthera'. The fruit is small to medium (0.9–1.6 kg), ovoid (when small) to conical and green, with a little yellow in the centre of the mature eyes (Fig. 3.4). The flesh is soft, white and juicy with an exquisite aroma. Its sugar (13–16°Brix) and ascorbic acid contents are high. As with most conical fruits, it shows a strong gradient of maturation from base to top. The plant is medium-sized and vigorous, with dark green, erect and spiny leaves. In some strains, long and erect basal slips surround the fruit. 'Pérola' is a very robust cultivar, showing resistance to *Phytophthora* (Collins, 1960), probably related to its erect habit, and tolerance to drought, mealybug wilt and nematodes (Collins and Hagan, 1932; Sipes and Schmitt, 1994; Sarah *et al.*, 1997). However, it is threatened because of its high susceptibility to fusariosis, which affects Brazilian production severely.

'Perolera', also named 'Lebrija', 'Motilona', 'Capachera' or 'Tachirense', is an

Fig. 3.4. 'Pérola'.

important cultivar of the north-eastern Andes of Colombia and Venezuela. The fruit is large (1.5–3 kg), yellow to orange, with an irregular cylindrical shape. It is borne on a long peduncle, which makes it susceptible to fruit lodging and sunburn, particularly in hot lowlands. The flesh is pale yellow to yellow, firm and sweet (although only around 12°Brix). Numerous crownlets protrude from the base of the crown and the upper eyes. Slips are also numerous (from four to 11). The plant is medium to high. The leaves are completely smooth because the lower epidermis is folded over the leaf edge, a trait that was named 'piping' by Collins and Kerns (1946). 'Perolera' is susceptible to fruitlet core rot and to the fly *Melanoloma canopilosum* Hendel. It has been used in the Brazilian breeding programme because of its resistance to fusariosis.

The cultivar 'Manzana' (Plate 12), also called 'Bumanguesa', is cultivated in the same zone as 'Perolera', as well as in the western

Fig. 3.5. 'Manzana'.

Andes of Colombia. It is said to be a sport from 'Perolera', from which it differs in the regular globular to cylindrical shape and large flat eyes of its fruit, which is of an attractive dark to bright red colour when produced in tropical highlands (Fig. 3.5). It is susceptible to the nematode *Pratylenchus neglectus* but tolerant to *Meloidogyne incognita* Kofoid & White (Redondo-Echeverri and Varón, 1992).

Other traditional cultivars of lesser regional importance are sometimes described. 'Cabezona' is a vigorous spiny triploid producing yellow to orange fruits of more than 3 kg with white pulp. 'Monte Lirio', also called 'Cambray' or 'Milagreña', is a smooth ('piping') cultivar with a mid-size fruit and sweet white pulp, found from Mexico to Ecuador. 'Black Antigua' is an old spiny cultivar producing a small to medium fruit with a dark green shell turning yellow to orange at maturity. Its golden-yellow pulp is firm and delicious. The Peruvian 'Samba' and 'Roja Trujillana' produce red fruits and show resistance to *S. basilides* (Bello *et al.*, 1997a). Certain Amazonian cultivars, such as 'Gigante de Tarauacá' or 'Cabeça de Onça', yield enormous fruits up to 15 kg (Ritzinger, 1987). Others are distinguished by an original red or purple colour of their fruit, such as the Amazonian 'Cabeça de Arara' (meaning 'Macaw Head') and 'Roxo de Tefé', the Trinidadian 'Mundo Nuevo Red' and the Venezuelan 'Morada'. These colours are very probably determined by a single dominant gene, as observed in the case of 'Roxo de Tefé' (Cabral *et al.*, 1997). Further evaluation of the germplasm recently collected in the basins of the Amazon and the Orinoco will provide many new traits of interest for varietal diversification.

The hybrid 'MD-2', 'Golden Ripe' or 'Extra Sweet' and its sibling 'CO-2' (US Patent PP8863) (Plate 13) were developed by Del Monte Fresh Produce Hawaii Inc. from a cross made between the PRI hybrids 58–1184 and 59–443 for the fresh-fruit market. 'MD-2' gives a medium to large (1.3–2.5 kg) cylindrical, square-shouldered fruit, with large flat eyes and an intense orange-yellow colour. The clear yellow pulp is sweet, compact and fibrous. It is high in sugar (15–17°Brix) and ascorbic acid but lower in total acid than 'Smooth Cayenne'. The core is tender, edible and thinner than in 'Smooth Cayenne'. However, the crown is larger and must be broken at harvest. The leaves are yellow-green with a reddish tip and are mostly spineless. 'MD-2' is said to be more productive than 'Smooth Cayenne'. It is resistant to internal browning, but susceptible to fruitlet core rot and more sensitive to *Phytophthora* than 'Smooth Cayenne' (Anon., 1996). 'CO-2' is said to resemble the parents, but is distinguished from them in being sweeter and higher in ascorbic acid and in having a 'distinct tropical flavour', greater pigmentation and fibre content of the flesh, greater resistance to internal browning and a good overall appearance after refrigerated storage.

'Josapine' (Plate 14) is a hybrid between 'Johor' ('Spanish') and 'Sarawak' ('Smooth Cayenne') released by MARDI in 1996 (Chan and Lee, 1996). It is recommended as a table

variety. It fruits very early and is cultivated on an annual cycle in Malaysia. The plant is vigorous and produces two to three shoots. Leaves are lightly purple-tinged, usually with spineless margins except for the leaf tip. Crowns are medium, occasionally with multiple proliferation. Fruits weigh between 1.1 and 1.3 kg and are cylindrical-shaped with dark purple peel ripening to an attractive orange-red (Fig. 3.6). The flesh is deep golden-yellow and has a strong aroma and a sugar content between 17°Brix on peat soil and 22°Brix on mineral soils. 'Josapine' fruits have a good storage life and are resistant to black-heart disorder or internal browning caused by low temperatures.

'Scarlett' is a hybrid between 'Smooth Cayenne' and 'Manzana' developed by CIRAD-FLHOR. Fruits are 1.4–2 kg and orange to red in colour, with a regular cylindrical shape. The eyes are medium to large and flat. The flesh is firm and golden-yellow with a high sugar content (15–18°Brix). Acidity is similar to that of 'Smooth Cayenne' but it is higher in ascorbic acid content. The core is thinner, the flesh less fibrous and the crown is lighter and erect. The plant is compact, with erect, smooth ('piping') leaves. The peduncle is long but resistant to lodging. 'Scarlett' has a short production cycle and responds well to floral induction. It is susceptible to fruitlet core rot (Coppens d'Eeckenbrugge and Marie, 2000).

Fig. 3.6. 'Josapine'.

Genetic resources from other species and botanical varieties

The wild pineapples, *Ananas comosus* var. *ananassoides* (Plate 2) and *A. comosus* var. *parguazensis* (Plate 4), constitute the main reservoir of genetic diversity. The former is generally considered the most drought-resistant pineapple. Its fruit is often seedy, with white to yellow pulp, which is firm and fibrous. Sugar and acid contents are high and it has a good flavour and aroma. The core is narrow. According to Collins (1960), crosses between *A. comosus* var. *comosus* and *A. comosus* var. *ananassoides* yield hybrids that are entirely comparable with crosses between cultivars, with highly variable sugar and acidity values. Mean acidity value is intermediate between those of the parents, but the average sugar content of the hybrids is much closer to that of the *A. comosus* var. *ananassoides* parent. *A. comosus* var. *ananassoides* is a potential source of resistance or tolerance to wilt, nematodes (*Meloidogyne javanica*, *Rotylenchulus reniformis*) and crown and root rot (Collins and Hagan, 1932; Hagan and Collins, 1932; Collins, 1960; Ayala, 1961; Ayala *et al*., 1969; Sipes and Schmitt, 1994). *A. comosus* var. *parguazensis* is less variable. It has a globular fruit with relatively wide flat eyes and a white and fibrous pulp. Resistance to fusariosis is variable in *A. comosus* var. *ananassoides* and *A. comosus* var. *parguazensis* (de Matos *et al*., 1991).

A. comosus var. *bracteatus* (Plate 6), first cultivated for the fruit and as a living fence, is now widely used as a tropical garden ornamental. Its variability is very limited. It

grows well on poor and dry soil and it is well adapted to cool conditions and altitude. The fruit is small to medium, with white fibrous flesh, a small core and an average sugar and acid content. It is resistant to heart rot, root rot and fusariosis (de Matos *et al*., 1991). Studies on nematode resistance produced contradictory results (Collins, 1960; Sipes and Schmitt, 1994). Crosses with *A. comosus* var. *comosus* yield hybrids with fruits of good size and weight and a wide variation in flavour (Collins, 1960).

A. comosus var. *erectifolius* (Plate 3) has been cultivated for its long and strong fibres. In the past decades, a dark red cultivar has also been exploited as an ornamental for the European cut-flower market. This trait is controlled by a single dominant gene (Cabral *et al*., 1997). The use of *A. comosus* var. *erectifolius* in breeding for dual-purpose (fruit and fibre) cultivars has been envisaged in the Philippines (V. Villegas, Fort-de-France, 1992, personal communication). *A. comosus* var. *erectifolius* is resistant to heart rot and root rot (Collins, 1960) and relatively tolerant to nematodes (Sipes and Schmitt, 1994).

Ananas macrodontes (Plate 1) has been mainly used as a source of fibre. As with all other pineapples, it is resistant to drought but it also tolerates temporary flooding. It is resistant to heart rot, root rot, wilt and fusariosis (Collins, 1960; de Matos *et al*., 1991). When selfed, *A. macrodontes* shows little variation, indicating that it is relatively homozygous (Collins, 1960). Hybridization with *A. comosus* var. *comosus* produces 5–10% fertile seeds, most of which are tetraploid. These tetraploids are fully fertile.

Breeding System

The breeding system of *A. comosus* combines efficient vegetative reproduction with functional allogamous sexual reproduction. Although the former is largely dominant, the latter is responsible for most of the present genetic variation. Pineapple allogamy, as well as its consequent heterozygosity, is related to the existence of self-incompatibility and pollination by hummingbirds. A high chromosome number also favours genetic recombination. *A. macrodontes* also combines vegetative and sexual reproduction, but apparently with a higher efficiency of the latter than in *A. comosus*, and it is not self-incompatible.

Cytogenetics

Chromosome number

Like many other *Bromeliaceae*, all the botanical varieties of *A. comosus* have a diploid number of 50 minute, almost spherical, chromosomes, with a length of 0.5–1.7 μm. Among three pineapple accessions, Sharma and Ghosh (1971) identified four chromosome types and observed a slight variation in their distribution and in chromatin content. They also observed secondary constrictions in two to five pairs of chromosomes. Arumuganathan and Earle (1991) reported values of 1.09 and 0.92 pg (corresponding to *c*. 526 and 444 Mbp) for the DNA content of 2C nuclei of *A. comosus* var. *comosus* and *A. comosus* var. *bracteatus*, respectively. Triploids (e.g. cultivars 'Cabezona', 'Caicara', 'Monte Oscuro'), tetraploids and even heteroploids (60 chromosomes) may also occur (Collins and Kerns, 1931; Canpinpin and Rotor, 1937; Collins, 1960; Antoni, 1983; Lin *et al*., 1987; Dujardin, 1991). Collins and Kerns (1931) reported six cases of triploidy out of 8000 plants resulting from a cross between 'Smooth Cayenne' and a clone of *A. comosus* var. *ananassoides*. Collins (1933b) demonstrated that these triploids had arisen from unreduced female egg cells fertilized by normal haploid pollen. Tetraploids could then be obtained from unreduced male and female gametes, although their occurrence is rarer than triploids. These tetraploids produce about 90% viable pollen, of a larger size than pollen cells of diploid plants. By crossing them with diploids, hybrid tetraploid seedlings were obtained, which grew faster and larger than diploids. *A. macrodontes* is a natural tetraploid with 100 chromosomes (Collins, 1960).

Ploidy level and morphology

Collins (1933b, 1960) and Kerns and Collins (1947) compared triploid and diploid

hybrids and diploid and autotetraploid plants of 'Smooth Cayenne'. The polyploids were taller, with wider leaves, placed at a greater internodal length, so the total leaf area does not differ much. The cross-section of the tetraploid leaves is more closed. Their larger fibres increase leaf rigidity. The size of cells, trichomes and stomata also increases with the ploidy level, while the stomata density is reduced. Water content is higher in polyploids. Triploid hybrids and tetraploid 'Smooth Cayenne' have longer vegetative growth periods, mature more slowly and have a lower fruit sugar content. Tetraploid fruits are smaller, with fewer but larger fruitlets.

Micro- and megagametogenesis and fertility

Meiosis is primarily regular in diploid and tetraploid *A. comosus*, as well as in *A. macrodontes*, with only rare irregularities, such as lagging chromosomes and some abnormal tetrads (Collins and Kerns, 1931; Canpinpin and Rotor, 1937; Collins, 1960). However, some irregular gametes are produced. The proportion of giant pollen cells may reach 6.5% and that of giant ovules 1%. Bhowmik (1977) observed large variations in size and fertility of pollen grains in 'Kew' ('Smooth Cayenne') and 'Queen' (from 35 to 81 μm and from 36 to 68 μm, respectively) and correlated them with the frequencies of univalents and secondary associations of up to three or seven bivalents in these cultivars. Pollen size and fertility also vary between cultivars and clones (Collins, 1960; Ramírez, 1966; Wee and Rao, 1979; Nayar *et al.*, 1981; Antoni, 1983; Coppens d'Eeckenbrugge *et al.*, 1993). Triploid genotypes are sterile because of irregular meiosis. Tetraploids produce 90% of good pollen grains, which are uniform but larger than those of diploids (Collins, 1960).

The number of ovules varies widely in *A. comosus*. While *A. comosus* var. *bracteatus* may have 40–70 ovules per flower, this number generally ranges from 14 to 30 in the wild botanical varieties and in *A. comosus* var. *erectifolius* and from 16 to 71 in *A. comosus* var. *comosus* (Coppens d'Eeckenbrugge *et al.*, 1993). There is also variation in all the species in the relative frequencies of anatropous and orthotropous ovules. The embryo sac develops according to the *Polygonum* type. Shrinking embryo sacs have been commonly observed at the eight-nucleate stage in 'Masmerah' (Rao and Wee, 1979) and the six main cultivars of *A. comosus* var. *comosus* and in *A. comosus* var. *ananassoides*, *A. comosus* var. *erectifolius* and *A. comosus* var. *bracteatus* (F. Van Miegroet, personal communication). The proportion of ovules with normal embryo sacs is correlated with the proportion of stained pollen and with fertility (F. Van Miegroet and Coppens d'Eeckenbrugge, unpublished results).

Fertility rate (i.e. the percentage of ovules producing a seed) is generally lower in *A. comosus* var. *comosus* than in the other botanical varieties. In the latter, fertility ranged from 6% (0.85 seeds per flower) in *A. comosus* var. *ananassoides* to 35% (18.4 seeds per flower) in *A. comosus* var. *bracteatus*. Within *A. comosus* var. *comosus*, the cultivars with 'piping' leaves often exhibit a higher fertility (4–11%; two to five seeds per flower) than the common cultivars 'Smooth Cayenne', 'Española Roja', 'Singapore Spanish', 'Pérola' and 'Queen' (less than 5%; zero to two seeds per flower). However, the highest fertility rate (29%; 9.45 seeds per flower), which is comparable to that of wild types, was observed in a spiny landrace. These fertility rates were estimated under an open-pollination situation and higher values may be expected under assisted pollination. Fertility is correlated with ovule fertility, pollen stainability and the amount of pollen produced per flower. It is not correlated with ovule number, probably due to crowding or competition effects between fertilized ovules. Indeed, many genotypes of *A. comosus* var. *comosus* and *A. comosus* var. *bracteatus* can develop only a small proportion of their numerous ovules into seeds (Coppens d'Eeckenbrugge *et al.*, 1993). Fertility may be affected by abnormal anthesis. Thus, in certain clones of 'Española Roja' and 'Singapore Spanish', a significant proportion of flowers do not open, hampering pollination.

Self-incompatibility

In *A. comosus*, the self-incompatibility is brought about by the inhibition of pollen-tube growth in the upper third of the style (Kerns, 1932; Majumder *et al.*, 1964). It is gametophytically controlled by a single locus with multiple alleles (Brewbaker and Gorrez, 1967) and is generally stronger in *A. comosus* var. *comosus* than in the other botanical varieties. Later work, however, suggested that more than one gene might be involved in the control of self-incompatibility (D.D.F. Williams, Colorado, 2001, personal communication). However, many cultivars exhibit pseudo-self-compatibility, expressed in the variable production of self-seeds, although the resulting self-fertility is always lower than cross-fertility. For instance, pseudo-self-incompatibility is common in 'Singapore Spanish', 'Perolera', 'Manzana', 'Primavera', 'Rondon', 'Cambray', 'Amarelo de Uaupés', 'Roxo de Tefé', 'Morada' and 'Alto Turi' and in some clones of 'Queen' (DeWald *et al.*, 1992; Coppens d'Eeckenbrugge *et al.*, 1993, 1997; Muller, 1994). In a sample of 84 clones from 51 cultivars and primitive landraces studied by Muller (1994), 55 appeared strongly self-incompatible and 21 pseudo-self-compatible and eight exhibited a self-fertility comparable to their fertility, which could be due to self-compatibility or a very weak self-incompatibility. Indeed, a dominant mutation suppresses the incompatibility reaction in the pollen of 'Smooth Cayenne' and results in the production of selfed seeds (Collins, 1960). The self-incompatibility of *A. comosus* var. *comosus* does not appear to be affected by tetraploidy (Kerns and Collins, 1947).

Pseudo-self-compatibility is more frequent in the wild pineapples. In Muller's study, five out of 11 *A. comosus* var. *ananassoides* clones and four out of seven *A. comosus* var. *parguazensis* clones exhibited pseudo-self-compatibility. One *A. comosus* var. *parguazensis* clone appeared self-compatible. In *A. comosus* var. *bracteatus*, three clones that were phenotypically identical appeared to be self-compatible. A variegated clone of the same species was self-incompatible, while another was pseudo-self-compatible. *A. macrodontes* is highly self-fertile and produces uniform progenies, suggesting that this species is autogamous.

Hybridization between botanical varieties and between species

There is little difficulty in crossing cultivars of *A. comosus* var. *comosus* with clones from the other botanical varieties. Instead, these crosses often show high fertility, as a result of higher gamete viability of the latter. When *A. comosus* is crossed with *A. macrodontes*, a few fertile seeds are produced, which usually yield vigorous tetraploids and sometimes self-sterile triploids. The tetraploid hybrids are highly fertile and self-fertile (Collins, 1960).

Breeding and Selection Techniques

Clonal selection and roguing

Many commercial pineapple cultivars are improved through selecting genetic variants that occur occasionally in experimental plots or production fields. Such variants are perpetuated as clones whose genetic make-up is identical and 'fixed' by vegetative propagation until new variation arises. Clonal plantings form the basis of modern pineapple culture, and many different clones are used throughout the world. All 'Smooth Cayenne' clones in Hawaii, including 'F200' and the 'Champaka' clones were developed through clonal selection (Py *et al.*, 1987). In Australia, clonal selection began in 1950 with the selection of 100 plants from commercial fields. Four clones – 'C8', 'C10', 'C13' and 'C30' – were eventually released to the industry in 1975 (Groszmann, 1982) and, in conjunction with the Hawaiian clone 'Champaka F180', form the basis of the present-day industry. Several clones of the cultivar 'Queen' have also been established in Australia, including 'Ripley Queen', 'Alexander' and 'McGregor', through a process of clonal selection by private growers (Lewcock, 1940). In Malaysia, an improved cultivar, 'Masmerah', with

higher vigour and yield, was obtained by clonal selection from a commercial field of 'Singapore Spanish' (Wee, 1974). Clonal selection has also been used in the Philippines to develop a new clone of 'Smooth Cayenne' less prone to the green-ripe disorder (Obrero, 1995).

Spontaneous mutations

At least 30 major mutations have been recorded in 'Smooth Cayenne' pineapple since the early 1920s. These include white flowers (as opposed to purple), foliar floret proliferation, multiple sepals and bracts, enlarged fruit segments, protruding fruit segments, increased or decreased trichome density, seediness, multiple crowns, a lower harvest index, misshapen fruits, smaller-diameter fruits, leaf spininess, reduced chlorophyll or anthocyanin levels, dwarfed habit, translucent fruits, collar of slips, increased or decreased slip number and fruits with an increased incidence of basal knobs (Anon., 1925, 1940; Kerns, 1928; Collins and Kerns, 1938; Groszmann, 1939; Dalldorf, 1975; Sanewski *et al*., 1992). Other measurable differences between clones likely to have been caused by mutations are sucker number, length of the fruit development period and peduncle length and width (Sanewski, 1997). Only two mutations – non-translucent fruit and resistance to mealybug wilt – could be considered substantially progressive (Collins and Carter, 1954; Obrero, 1995). Mutations can also be induced with a range of techniques, including tissue culture (Williams and Fleisch, 1993), exposure of *in vitro* leaf cultures to cobalt gamma rays (Cisneros *et al*., 1998) and the treatment of seed and plants with chemical mutagens (Singh and Iyer, 1997).

Despite the large number of mutations identified in pineapple cultivars, they are not generally considered to be unstable genotypes. The incidence of mutations is probably a function of the large number of plants propagated and observed. The type of planting material used may also determine the frequency of some off-types. As an example, if slips are used as planting material, then plants that produce the mutation near-collar (slips arise from the peduncle very close to the base of the fruit) will be multiplied faster than normal types and hence the frequency will increase. Therefore, while the genotype is considered stable, some specific characters, such as leaf spininess, are considered unstable and the frequency of mutation for these characters is high (Collins and Kerns, 1938).

Roguing

As most mutations are regressive and considered to be off-types, the population performance will gradually decline if no selection is done to maintain its standards. Inferior types may be difficult to detect visually, especially those that have slightly reduced plant vigour or fruit size. With the large number of plants grown and the efficient propagation methods used, inferior types that escape detection can be quickly multiplied. Roguing can rapidly reduce the percentage of most off-types, where they are initially numerous, to low levels. Therefore, major pineapple producers routinely rogue inferior spontaneous mutants to maintain productivity and efficiency.

Roguing is sometimes called mass selection, although, strictly speaking, it is a form of culling rather than selection. Roguing aims to minimize the number of undesirable variants in a field by not replanting material from those plants. Roguing is, by necessity, an ongoing process and is best performed on well-grown plant crops. To identify the inferior plants the grower walks through the field before harvest and marks the crown or plant itself with paint. The exact process will depend on what type of planting material is used. In Australia, it is performed on summer plant crops, where the expression of defects such as collar of slips is greatest (Groszmann, 1945). The main characteristics targeted in roguing are described below.

FRUIT WEIGHT. Fruit weight is strongly affected by environment and cultural operations. Also, subjective assessment of fruit weight in the field is difficult even where the differences are as much as 10%. For these reasons, roguing against decreased fruit weight is considered not to be very effective

(Kerns, 1928). There is, however, a tendency for the very heavy and very light types within a field to be genetically different. Roguing can therefore be used to discriminate against very small-fruited types (Anon., 1925). Where more objective methods of assessment of fruit weight are used, such as in a clonal selection programme, gains in fruit weight are possible, provided measures are taken to avoid inadvertent selection for more translucent types. As an example, a 10–15% increase in fruit weight was achieved in the Australian clonal selection programme (Wassman, 1982).

MULTIPLE CROWNS. Multiple or fasciated crowns can be heritable but the trait is also strongly influenced by environment and cultural operations (Dalldorf, 1975). Excessive nitrogen fertilization and high temperature during flower-cone development are known to increase the incidence of multiple crowns (Anon., 1925; Linford and Spiegelberg, 1933). Linford and Spiegelberg (1933) observed that the condition can start at the top of the fruit or, as evidenced by the change in eye pattern, at a position in the fruit itself. Replanting only single crowns from vigorously growing plants that flowered during the hotter periods of the year should reduce its incidence (Dalldorf, 1975). Roguing cannot completely eliminate this disorder.

COLLAR OF SLIPS AND KNOBBINESS. Collar of slips is a condition where several slips emerge from the base of the fruit. This severe defect is caused by a dominant mutation (Collins and Kerns, 1938). The incidence of knobs on the base of the fruit is closely associated with collar of slips and is sometimes considered a milder expression. Collar of slips is highly heritable but influenced by environment. In Australia, collar of slips is usually expressed in summer fruit but not winter fruit (Groszmann, 1940). Also, plants propagated from the collar-of-slips type will occasionally produce about 10% normal types (Collins, 1933a; Groszmann, 1945). Fruit from collar-of-slips types is usually smaller and slip number is more than double that of normal plants (Collins, 1933a; Py *et al*., 1987). It is best to avoid using slips as planting material unless the parent plants have been checked before harvest for the incidence of collar of slips. Eliminating this off-type should minimize its incidence. Collar of slips is one of the main characteristics targeted in a roguing programme (Py *et al*., 1987).

The number of slips produced lower down on the peduncle is not considered the same as collar of slips, as it is a quantitative trait whose expression is more strongly influenced by plant vigour and environment (Collins and Kerns, 1950). Vigorous plants on the outer edges of fields commonly produce more slips. The clone 'F200', which is grown widely in the Philippines, reputedly does not produce slips. Roguing against increased or decreased slip number is not likely to make much difference, because of the large environmental and cultural influences. However, a well-conceived clonal selection programme should make progress in this regard.

FRUIT CONFORMITY. There are several distinct mutations that affect fruit shape or appearance. Long Tom or long, slender fruits is a heritable condition where the fruits are long with a small diameter. Other common mutations in fruit conformity include dry fruit and bottleneck. With these off-types, the flowers are absent from either the upper portion of the fruit or the entire fruit. The effect is a small malformed fruit with obvious bracts but poorly developed eyes. These genetic disorders should not be confused with the physiological disorder associated with sun damage (Broadley *et al*., 1993). Roguing against these off-types should eventually eliminate them.

SPINY LEAVES. Genetic studies have shown that spiny leaf is recessive to smooth leaf and 'Smooth Cayenne' carries the gene for spines in a recessive condition (Collins and Kerns, 1946). The mutation of the dominant gene for smooth leaves to the recessive gene for spines can occur at any time in the growth of the plant. Depending on the developmental stage of the plant when the mutation occurs and the position in the plant of the mutating cell, it can result in a chimera with partially spiny leaves or a completely spiny plant (Collins and Kerns, 1933).

The mutation to spiny leaves should not be confused with the tendency of 'Smooth Cayenne' to develop spines as a result of stressful conditions and the cessation of leaf growth. As an example, a high night temperature increases the development of spines along the leaf (Friend, 1981). A genetic change is not thought to have occurred in these instances and new leaves develop normally once the growing conditions are favourable. Roguing is very effective in removing spiny-leaf off-types.

Clonal selection

While roguing is a form of clonal maintenance, clonal selection offers the possibility of clonal improvement. Clonal selection aims to identify superior individual plants that are eventually multiplied as a new clone. Clonal selection, however, is a slow process and is usually beyond the resources of the commercial grower.

It has been demonstrated that apparently normal plants can carry some undesirable traits, such as multiple crown. If enough plants of that genotype are observed over several environments, these traits will eventually be expressed and that line or clone can be eliminated. Clonal selection is therefore more successful than roguing against defects such as multiple crowns that are strongly influenced by environment.

The initial population in a clonal-selection programme is established usually by walking through fields of maturing pineapples and selecting the crown from superior types or marking the plant with paint and a stake to collect the entire plant later. These selections are then assessed and multiplied over several crops until only the most consistent clones remain. When sufficient plants are available, replicated trials can be established in different environments. The method of obtaining the initial population will, of course, vary depending on the specific characters in which the breeder is most interested. Novel methods of selection can be used for some traits. As an example, a different approach to selecting for larger-fruited types has recently been used in the Australian clonal-selection programme. Selection of larger-fruited types by sorting several thousand fruit using a weight grader appears more reliable than walking through fields and selecting plants by subjective assessment of fruit weight (G.M. Sanewski, unpublished results).

Hybridization

Cultivated pineapple is self-incompatible but sets seeds readily when cultivars from different groups are crossed. Pineapple cultivars are heterozygous, and hybridization is a valuable method in generating widely variable genotypes through gene recombination. With clear objectives and judicious selection of the parents, the hybrid population would present a spectrum of variation within which the desired improved genotypes may be found. It was believed that many important characteristics, such as high carotene content, greater translucency and lower acidity, that could not be achieved by clonal selection could be realized by hybridization (Wortman and Kerns, 1959).

Considerations in hybridization

FERTILITY, COMPATIBILITY AND DIRECTION OF CROSS. Fertility and compatibility are important considerations in deciding the parents to be used for hybridization and also the direction of the cross, i.e. deciding which parent should be paternal or maternal. Chan (1986) found that, for crosses between 'Smooth Cayenne', 'Queen', 'Singapore Spanish' and 'Johor', a hybrid between 'Smooth Cayenne' and 'Singapore Spanish' was compatible, but there was differential seed set between the crosses and their reciprocals. 'Smooth Cayenne', for instance, has low fertility and was a poor female parent because only a few seeds were formed. However, reciprocal crosses using 'Smooth Cayenne' as the pollen donor provided satisfactory seed set in all crosses. In the extreme case, the 'Smooth Cayenne' female crossed with 'Johor' was incompatible but the reciprocal produced about 1000 seeds in a well-pollinated fruit (Chan, 1986). 'Smooth Cayenne' was also shown to be a poor female parent, bearing only about 200 seeds per fruit. When a reciprocal cross was made with the

much more fertile 'Perolera' as the female parent, there were more than 2000 seeds per fruit (Cabral *et al.*, 1993).

The direction of the cross was reported by Loison-Cabot and Lacoeuilhe (1990) to have an influence on the performance of the hybrids. In a cross between 'Smooth Cayenne' and 'Manzana', the latter used as the female parent improved the yield of the hybrid population compared with the reciprocal. In the case of total soluble solids (TSS), 'Smooth Cayenne' as the female parent generated progenies with higher TSS content.

SYNCHRONY IN FLOWERING. Synchrony in flowering of parents is obviously an important consideration in hybridization. The time taken for appearance of red-heart from time of hormoning is variable between various pineapple cultivars. Inflorescence appearance in 'Smooth Cayenne' is 10–12 days later than in 'Singapore Spanish' and 'Queen', respectively. This means that, while 'Singapore Spanish' and 'Queen' may be induced to flower simultaneously, 'Smooth Cayenne' should be induced about 2 weeks earlier in order that inflorescences of all varieties appear simultaneously for hybridization. Where the time to anthesis is unknown for each parent cultivar, a percentage of plants of each cultivar should be induced at, say, 5-day intervals.

TIME OF DAY FOR HYBRIDIZATION. Dawn to 9 a.m. is probably the best time for pollination (Cabral *et al.*, 1993; Sanewski, 1998). However, pollination may be done during the entire length of the day, although seed set may vary depending on the time of day and appears to be temperature-related (Chan, 1986). Higher seed set was obtained when crossing was done during the early morning or cooler evening and a significantly lower seed set when it was done during the hotter midday or early afternoon.

SEGREGATION IN HYBRID POPULATIONS. Evaluation of hybrid populations from biparental hybridization indicated that there is wide segregation of progenies for most quantitative characters (Chan, 1989, 1991; Loison-Cabot, 1990; Sanewski, 1998). For TSS, for example, the range of values showed transgressive segregation, i.e. the minimum and maximum values of the hybrid progenies exceeded the lowest and highest values of both parents. Sanewski (1998) reported that the range of TSS from hybrids of the 'Queen' × 'Smooth Cayenne' cross was 9–24%, while the parents had a narrower range of 14–19%. The coefficients of variance in the hybrid population for many quantitative traits quite often exceeded twice that of the parents (Chan, 1989, 1991). As a matter of fact, the variation generated through hybridization of even closely related cultivars may be as large as that obtained for some pineapple collections (Chan, 1989). This wide variation will provide good opportunities for selection of improved recombinants.

Choosing the most suitable parents

In hybridization for improvement of pineapple, the choice of parents has usually been based on the strength of one in complementing the weakness of the other. For example, the ascorbic acid content of 'Smooth Cayenne' is improved using 'Perolera' ('Manzana'), which has higher ascorbic acid (Loison-Cabot, 1987), and 'Queen' for increasing TSS of 'Smooth Cayenne' winter fruits (Winks *et al.*, 1985). Where biparental crosses are focused narrowly on the improvement of a single character, there is danger that the donor parent might inadvertently introduce other adverse characters.

In practice, breeders are always faced with selection of a set of economic traits and not just single characters. In this case, selection of suitable parents may be complicated. Chan (1991) computed breeding values for parents based on consideration of eight agronomic characters. The values were computed by obtaining the product of the percentage of progenies that qualified for selection in each of the eight characters. 'Queen' and 'Smooth Cayenne' were better all-round parents for hybridization because 1.1–1.2 % of the progenies qualified for selection when eight characters were considered. This was twice as much compared with the 'Singapore Spanish' parent. Sanewski (1998) used a similar computation and found that advanced

hybrids, such as '73–50' developed by PRI, had a high breeding value. Sanewski (1998) concluded that these hybrids are valuable as parents because they have accumulated desirable genes during earlier multiple crossings and subsequent selection. Breeding values are helpful for guidance in the choice of parents and in ascertaining the probability of obtaining useful progenies. They are also useful for determining the population size of the hybrid progenies. Quite evidently, higher breeding values of parents will yield higher percentages of promising hybrids, thereby reducing the need for larger populations.

The high level of heterozygosity of pineapple cultivars reduces the chances of quickly obtaining progenies with a large complement of specific characteristics and it is this heterozygosity that is largely responsible for the slow rate of progress in most breeding programmes. Strategies such as selfing (Cabral *et al*., 2000), backcrossing and sib-crossing need to be investigated more thoroughly, especially considering the demonstrated inefficiencies of combining heterozygous genotypes. Other strategies to circumvent the heterozygosity of potential parents such as the development of homozygous haploid parents by anther and ovule culture have now been reported (Benega *et al*., 1998a; Cabral *et al*., 2000).

Suitable hybrid population size

Hybridization produces recombinants, but potential selections that meet all the selection criteria of the breeder will appear very rarely. Therefore, very large populations are usually required to increase the chances in the draw of this genetic lottery. With the breeding values of parents known, the population size that may be required can be estimated (Chan, 1991). The number of selections in the second cycle that the breeder would want to evaluate must first be ascertained. At MARDI, it was put at 300 selections and hybrid populations of 23,000–45,000 progenies, depending on the parents' breeding values, will be needed to have a realistic chance that the desired number of potential recombinants would be generated. Loison-Cabot (1987), using 'Smooth Cayenne' and 'Perolera' parents, recommended 30,000 progenies for each annual selection cycle, while Cabral *et al*. (1993) and Benega *et al*. (1998b) maintained 23,000 and 34,000 progenies, respectively, to obtain 120–169 first-cycle selections. The PRI breeding programme has been the most extensive to date and, at its peak, was producing over 1 million seedlings per year. Up to 100,000 seedlings were developed from some of the better parent combinations (Williams and Fleisch, 1993). Sanewski (1998), using some of these PRI selections, obtained 300 selections from populations of 50,000 seedlings because the parents have very high breeding values.

Some interest has been shown in the use of other species for imparting characteristics such as disease resistance. Collins (1960) indicated that, where crosses with wild germplasm were performed, only 1000 progenies were necessary in the first generation but 15,000–25,000 per backcross were required for each of four backcross generations.

Crossing technique

Pollen is collected from flowers at anthesis early in the morning. The flowers are removed from the inflorescence by making three deep triangular incisions into the base of the flower and then gouging them out. This method of collecting pollen from excised flowers is better than removing only the stamens. Pollen in excised flowers should stay fresh longer and dehydrates less rapidly. There are no conclusive data on the storage of pollen, but Kerns (1931) indicated that 'Smooth Cayenne' pollen could be stored in cool, dry air for 15 days with minimal loss of viability.

During hand-pollination, the petals of the flower are removed to expose the freshly dehisced anthers with an abundance of pollen. The anther is picked up with a fine pair of forceps and gently brushed on to the stigma of the flower to be pollinated. In most cases, there is no necessity to emasculate the flowers before pollination because most cultivars are self-incompatible. In cases where fidelity of the pollen source is vital, as in genetic studies, or when natural pollinators

are present, the contamination of foreign pollen can be prevented by using a fine mosquito netting or paper bag placed over the inflorescence (Leal and Coppens d'Eeckenbrugge, 1996). Depending on varieties, the number of flowers in an inflorescence ranges between 75 and 150. About three to seven flowers open daily and 2–3 weeks may be required to complete pollination of the whole inflorescence (Chan, 1986).

Inbreeding

The difficulty in finding a superior recombinant among the widely varying progenies obtained through direct hybridization of highly heterozygous pineapple cultivars is the main cause of the failure of many breeding programmes (Collins, 1960; Williams and Fleisch, 1993; Coppens d'Eeckenbrugge and Duval, 1995). This led some researchers to evaluate the potential of inbreeding in pineapple breeding. Thus, Collins (1960) selfed a mutant of 'Smooth Cayenne' and observed in the resulting progenies a loss of vigour and a wide range of variation for qualitative and quantitative traits. In the second generation, inbreeding depression was so severe that only a few plants produced fruits and none of them set seed. Backcrosses of first-generation inbreds to 'Smooth Cayenne' restored vigour. Collins (1960) suggested the possibility of using this method to synthesize new cultivars very similar to 'Smooth Cayenne'. Following a similar idea, Coppens d'Eeckenbrugge and Duval (1995) proposed the introduction of one cycle of selfing before the final hybridization to produce inbred genotypes from the parental cultivars. Crossing genotypes with 50% homozygosity would considerably lower the variability of the hybrid progeny. In addition, studies on segregation of selfed progenies would provide specific information on the genetic nature of the parental cultivars, allowing identification and selection of recessive favourable alleles and elimination of codominant and recessive unfavourable alleles. The final hybridization between the best inbreds from two different cultivars would restore vigour.

In pseudo-self-compatible cultivars, a few inflorescences would be sufficient to obtain the small number of self-seeds required. In addition, selfing is much less labour-intensive than crossing since these few seeds can be obtained by simply bagging the inflorescence before anthesis (Coppens d'Eeckenbrugge *et al.*, 1993). However, for strongly self-incompatible cultivars, a high number of selfings may be necessary. Attempts have been made to overcome self-incompatibility with X-rays (Marr, 1964) or gamma rays (Subramanian *et al.*, 1981). Bhowmik and Bhagabati (1975) tested bud pollination, style-grafting and naphthalene acetic acid (NAA) application, but only the last technique produced a few self-seeds in 'Queen'. Others have proposed obtaining homozygous plants through the production of doubled haploids. However, Collins's results throw some doubt on the viability of this approach. Highly depressed and sterile homozygotes obtained through this method would be of little use for breeding.

Coppens d'Eeckenbrugge *et al.* (1993) observed similar seed abortion rates after self- and open pollination of 71 cultivated and wild clones, which indicates no depression effect at the zygotic or embryonic level. No difference was observed in germination of self- and cross-seeds or in the early development of the resulting seedlings from 'Española Roja', 'Primavera', two clones of *A. comosus* var. *ananassoides* and two clones of *A. comosus* var. *bracteatus*. When transplanted to the field, these seedlings showed about 50% size reduction compared with progenies from open pollination. In contrast, a strong growth depression was observed in the early development of seedlings of self-progenies from 'Manzana' and from a clone of *A. comosus* var. *ananassoides*, causing their death in the nursery.

Progeny evaluation

Seed handling, germination and nursery management

Seeds can be harvested when fruits are ripe. Seeds develop in the ovarian cavities (eyes) and the cavities can be exposed by cutting

the peel of the fruit to a depth of about 1.5 cm. The exposed seeds in the cavities are scraped out and washed. Alternatively, seeds can be extracted from the pulp using a low-speed blender, preferably with a plastic blade. Most non-viable seeds are empty and remain afloat and these can be eliminated with the rinse water. Clean seeds are disinfected with 2–3% sodium hypochlorite and a wetting agent, dried and treated with a suitable fungicide before storage. The use of a fungicide is critical. Storage of seeds with silica gel in sealed plastic bags in a refrigerator at 4–5°C can maintain viability for 2 years (Leal and Coppens d'Eeckenbrugge, 1996).

Seed pretreatment with concentrated sulphuric acid for 30 s improves uniformity in germination (Collins, 1960) but is not essential. In the tropics, good germination can be obtained by sowing seeds evenly in shallow trays filled with fine river-sand. The trays are covered with clear polyethylene sheets to retain high humidity (Chan, 1986). In countries with cooler temperatures, germination in temperature-controlled glasshouses or in heated mist-beds inside a shade-house may be required (Sanewski, 1998). A range of different temperatures, from 24 to 35°C, have been used to germinate seed (Iyer *et al.*, 1978). Seeds can also be sown on sterile agar medium in culture rooms (Loison-Cabot, 1987; Benega *et al.*, 1997). Germination occurs normally after 2 weeks. The germination percentage of healthy bold seeds is generally 80% or more.

When the seedlings reach the sixth- to eighth-leaf stage after 3 months, they are either potted or carefully transplanted to peat beds in the nursery. During transplanting, some preliminary selection may be carried out to cull the obviously undesirable characters, such as poor vigour, albinism and spiny leaves. The seedlings are kept in the nursery for 6–12 months before they are transplanted in the field for evaluation. The simplest approach is to plant in blocks coded by the respective parent combinations. About 2% of the population are planted with check plants, usually the parents, interspersed randomly within the block (Sanewski, 1998). More complex designs can be used where parent combinations are being compared.

Field trials

In hybrid or inbred populations, each individual plant is unique and the segregation is very wide, but less so for inbred progenies. Evaluation is carried out on each plant and this may be very tedious considering the large populations that are normally grown. For this reason, only minimal data, covering mostly qualitative characters that can be visually recorded, are given emphasis. At this level of evaluation, basic data on fruit shape, fruit weight, flesh colour and probably TSS, quickly recorded with a hand refractometer, are collected. Plants with obvious defects, such as fasciated fruits, multiple crowns, collar of slips, conical fruits and long peduncles, likely to lead to fruit lodging, are eliminated. The individual selected plants are usually propagated to some extent, depending on the resources available. One approach is to use the leaf-bud technique to propagate from the crown, suckers, slips and stem, with each of the selections kept as a separate family. It should be possible to obtain up to 100 plants if all materials are utilized. A less intensive approach is to replant the crown, slips, suckers and stem sections only.

In the second round of selection, the selected families (clones) are further evaluated in replicated trials and more agronomic characters, such as ascorbic acid, fruit titratable acid, incidence of diseases and flavour, are recorded. In the Hawaiian programme, screening techniques for the most important diseases were applied by the third asexual generation. Subsequent selections based on clonal performance and not individual plant performance are made. Obviously poor-performing clones are discarded and, depending on management capabilities, up to ten clones will make the next important selection round, which is the genotype × environment trial. At this stage of testing, more materials are available from propagation of leaf buds obtained from plants in the selected clones. Tissue culture can also be used to great advantage at this stage. This penultimate stage of testing is carried out over a few diverse environments and the selected families are tested with contemporary commer-

cial varieties. The results of these trials will indicate the performance and stability of the selections compared with standard cultivars (Chan, 1997).

In Malaysia, the hybridization programme took about 12 years before release of the new variety 'Josapine'. Started in 1984 with the diallele cross of four cultivars, the progeny evaluation and selection went through four cycles before the potential selection was identified in 1993 (Chan, 1993). It took another 3 years to build up sufficient planting materials before the variety was released in 1996 (Chan and Lee, 1996). Loison-Cabot (1987) estimated that it would require 15 years to develop hybrid varieties for growers, the major part of the time being spent on evaluation trials and *in vitro* propagation of planting materials. Collins (1960) estimated that 20–25 years would be required for the development of commercially acceptable hybrids involving wild germplasm because of the need to incorporate about four additional back-crosses.

Prospects

A historical review of pineapple-breeding research showed that many breeders are quite content with working around the benchmark 'Smooth Cayenne' cultivar, focusing on improving specific weakness, such as disease and pest resistance, improving winter-fruit quality, peel colour and resistance to black-heart disorder. However, in the process of introducing the desired foreign gene from another variety through hybridization, many other undesirable attributes are introduced as well. This is particularly true when the source of the resistance gene is a wild relative with poor agronomic traits. Good selections in the segregating hybrid population in this case are expected to be extremely rare and this explains the lack of success in hybridization programmes. Better progenies are often obtained in back-crosses or between crosses involving inbreds or selected hybrids, as these procedures add on favourable genes to produce less variable but more useful hybrid populations. Sanewski (1998) reported that the PRI hybrids, such as '73–50', have high breeding values and make very good parents because they have accumulated desirable genes in their previous selection. It is envisaged that progress in hybridization should increase dramatically in the future as breeding programmes move beyond the basic-type crosses and into interhybrid combinations. However, it can be concluded that hybridization, with its attendant invasive arrangement in gene constitution of an established variety, is a long and tedious method, whose success depends, to a large extent, on the genetic lottery of a favourable recombinant.

Improvement of pineapple varieties should also involve techniques that are less invasive in genetic changes to the established cultivar. Spontaneous mutations (or 'spots') in the field or deliberately caused somaclonal variants during tissue culture are some ways in which small, favourable changes may be made to a standard cultivar. The prospects of genetically engineering target modifications to the host variety appear very promising. This area of research is already in progress for developing resistance to black-heart disorder and mealybug wilt, resolving precocious flowering and delaying ripening of fruit for extension of storage life. It would also be useful to obtain herbicide resistance in pineapple for ease of weed management. Genetic engineering must be supported by adequate gene mapping of the pineapple chromosomes. Present understanding in this area is still inadequate in locating, isolating and transferring genes in pineapple. Even with successful gene transfer, the task of field testing under biosafety regulations for genetically modified organisms will take many years to complete. It can be expected that there will still be non-governmental organization (NGO) groups and consumers in the European Union (EU) resistant to accepting genetically modified organisms. All these difficulties aside, genetic engineering is expected to be the tool to fine-tune the performance of current pineapple cultivars.

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4 Biotechnology

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Plant biotechnology is a new and rapidly developing discipline that offers substantial opportunities in the field of plant identification, multiplication and genetic improvement. The new tools of biotechnology have made it possible to excise precise lengths of DNA, to isolate and recombine them with other pieces of DNA, to move them around in DNA plasmids or vectors and to transfer the vectors into the same or other species in ways that permit the desired DNA to become part of the new organism.

Plant tissue culture is an integral part of plant biotechnology and includes the culture of plant cells, tissues or organs under aseptic conditions. This term can also be extended to include the culture of excised embryos and protoplasts. Transformation develops the tissue culture process further by delivering recombinant DNA to plant cells and the regeneration of plants from these cells. The goal of transformation is to 'engineer' plants that express the gene of interest without altering the remaining, and often unique, part of the genotype.

Tissue Culture

Smith and Drew (1990) have reviewed many of the applications of tissue culture for plant propagation and improvement. Applications for pineapple propagation and improvement include: micropropagation via axillary-bud proliferation, adventitious-bud proliferation and regeneration from callus cultures, *in vitro* germplasm conservation, and culture of excised protoplasts, ovules or anthers.

Micropropagation

Most tissue culture research in pineapples relates to the use of micropropagation for the rapid multiplication of cultivars. This has been stimulated by the relatively slow procedures currently used for clonal propagation and the large and regular demand for planting material. Traditional methods of pineapple propagation usually produce up to ten plants using crowns, slips and suckers from a single plant in a year. Sectioning of these components, including the stem, can deliver up to 100 plants. The chemical chlorfurenol can be used in commercial situations to enhance slip production as much as 30-fold. But, for sheer scale of multiplication, none compares with tissue culture, where, according to Pannetier and Lanaud (1976), 1 million plants could theoretically be achieved in 2 years from a single axillary bud.

The first report of pineapple *in vitro* propagation comes from the work of Aghion and Beauchesne (1960), and many of the earlier studies (Mapes, 1973; Mathews *et al*., 1976; Drew, 1980) concentrated on culture estab-

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lishment and the ability to take plants successfully through the micropropagation process. Subsequent studies have concentrated on methods to optimize multiplication, and today pineapple micropropagation is being used commercially in the pineapple industry to rapidly multiply important cultivars (Smith and Drew, 1990). In practice, micropropagation is used for the establishment of multiplication blocks, which then provide conventional planting material for larger production blocks. This is because micropropagated plants are more expensive and there are grower concerns about genetic off-types (somaclonal variants). The initial limited use of micropropagation in the multiplication of new cultivars allows screening of variants on fruit characteristics before conventional methods of multiplication are used.

Table 4.1 summarizes some of the methods developed for pineapple micropropagation. The most common explant used to initiate cultures is the axillary bud dissected from crown leaves. Fitchet (1990) also suggests that the crowns of some cultivars, such as 'Smooth Cayenne', should first be desiccated for a short period to break bud dormancy. Even though contamination of the initial cultures is common, owing to the closely packed whorl of leaves in the crown which traps water and airborne particles, enough buds can be obtained to ensure successful establishment of some explants following surface disinfestation. 'Clean' buds are most commonly grown on a Murashige and Skoog (1962) (MS) solid medium supplemented with a cytokinin, usually benzyladenine (BA), at between 2 and 5 mg l^{-1}. Using these concentrations with a cultivar such as 'Smooth Cayenne', ten to 15 plants per month can be produced. Multiplication may be enhanced two- to threefold by the use of agitated liquid media (Mathews and Rangan, 1979; DeWald *et al.*, 1988; Moore *et al.*, 1992), and further refinements have been made by the use of temporary immersion systems (Firoozabady *et al.*, 1995; Escalona *et al.*, 1998). A novel micropropagation method was developed by Kiss *et al.* (1995); this involved the induction of etiolated shoots, with subsequent multiplication of shoots along the nodal segments when placed horizontally on the culture medium.

Once shoots have been produced and multiplied, they are usually transferred to an MS solid medium containing an auxin, such as indole butyric acid (IBA), at between 0.5 and 2.0 mg l^{-1}, or to a hormone-free medium for root development. Plants can be successfully established in a soilless potting mix and 'hardened off' in the glasshouse prior to field establishment. The use of *Azobacter* or endomycorrhizal fungi has also been suggested as a way of improving the growth of micropropagated plants (Gonzales *et al.*, 1996; Guillemin *et al.*, 1996; Matos *et al.*, 1996).

Plants can also be regenerated from cell or callus cultures. When the cytokinin is supplemented with an auxin, such as naphthalene acetic acid (NAA), the development of 'lumpy' tissue with protocorm-like bodies, or callus tissue can result (Mathews and Rangan, 1979, 1981; Wakasa, 1989; Devi *et al.*, 1997). Proliferation of these types of tissue often results in cultures with an enhanced regeneration capacity via either organogenesis (Fitchet, 1990) or embryogenesis (Daquinta *et al.*, 1996; Cisneros *et al.*, 1998). Regeneration of plants from cell and callus cultures opens up possibilities for the genetic transformation of pineapples. However, these procedures must be viewed very cautiously because of perceived problems with somaclonal variation. As Scowcroft (1984) pointed out, as regeneration proceeds from more organized structures (axillary buds) to unorganized tissues (callus), the propensity of the cells to undergo genetic changes increases.

Somaclonal variation

Even though pineapple is not generally considered to have an unstable genotype, at least 30 mutants have been recorded in 'Smooth Cayenne' since the early 1920s (Collins and Kerns, 1938). Spiny leaves are commonly encountered during conventional pineapple propagation of 'Smooth Cayenne', and it is no surprise that spininess is also most commonly encountered during micro-

Table 4.1. Review of methods used for the micropropagation of pineapple.

Stage I		Stage II		Stage III		Stage IV	Reference
Explant	Axillary and terminal buds from crown	Medium	MS with 2.0 mg l^{-1} KIN, 2.0 mg l^{-1} IBA and 1.8 mg l^{-1} NAA 8 plantlets per month	Medium	MS with 0.1 mg l^{-1} NAA and 0.4 mg l^{-1} IBA	'Soil'	Mathews *et al.* (1976)
Medium	Nitsch with 0.1 mg l^{-1} BA and 0.1 mg l^{-1} NAA						
Explant	Axillary buds from slips and suckers	Medium	MS with 2.3 mg l^{-1} BA and 2.2 mg l^{-1} KIN 50 plantlets per month (callus involved)	Not stated		'Gro-pots'	Drew (1980)
Medium	MS, hormone-free						
Explant	Axillary bud from crown	Medium	MS with between 0.5 and 1.0 mg l^{-1} BA 3 plantlets per month	Medium	$\frac{1}{2}$ MS, hormone-free	Not stated	Zepeda and Sagawa (1981)
Medium	MS with 25% coconut water						
Explant	Axillary bud from crown	Medium	As for stage I, but liquid (shaken) cultures 17 plantlets per month for 'Smooth Cayenne'; 76 plantlets per month for 'Perolera'	No roots		'Commercial soil mix' Plantlets $>$ 2.5 cm	DeWald *et al.* (1988) Moore *et al.* (1992)
Medium	MS with 2 mg l^{-1}BA and 2 mg l^{-1} NAA						
Explant	Axillary bud from crown	Medium	MS with 0.5 mg l^{-1} BA 'Plantlets halved or quartered during subculture' 10 plantlets per month	Medium	MS, hormone-free	'Peat/perlite mix' Plantlets 2–3 cm	Cote *et al.* (1991)
Medium	MS with 0.5 mg l^{-1} BA and 0.2 mg l^{-1} IAA						

Continued

Table 4.1. *Continued*

Stage I		Stage II		Stage III		Stage IV	Reference
Explant Medium	Axillary bud from crown MT with 2.0 mg l^{-1} KIN, IBA and NAA	Medium	MT with 2.0 mg l^{-1} KIN and NAA 14 plantlets per month	Medium	MT with 1.0 mg l^{-1} NAA and 500 mg l^{-1} malt extract	'Peat/perlite/sand'	Fitchet (1990) Fitchet-Purnell (1993)
Explant Medium	Axillary bud from stem MS with 2.3 mg l^{-1} BA and 0.6 mg l^{-1} NAA	Medium	As for stage I 8 plantlets per month	Medium	MS with 0.3 mg l^{-1} IBA and 0.1 mg l^{-1} IAA	Not stated	Osei-Kofi and Adachi (1993)
Explant Medium	*In vitro* plantlets MS with 2.0 mg l^{-1} NAA in the dark	Medium	N6 with 5 mg l^{-1} KIN and 4.5 mg l^{-1} BA 'Etiolated shoots placed horizontally on medium' 60 plantlets per month	Medium	MS, hormone-free	'Soil' Plantlets 8 cm	Kiss *et al.* (1995)
Explant Medium	Apical bud from crown MS with 1.0 mg l^{-1} BA and 0.1 mg l^{-1} NAA	Medium	As for stage I, except 2.0 mg l^{-1} BA 'Regeneration from proliferating callus at base of plantlets' 56 plantlets per month	Medium	MS with 2.0 mg l^{-1} IBA	Not stated	Devi *et al.* (1997)

BA, benzyladenine; IAA, indole acetic acid; IBA, indole butyric acid; KIN, kinetin; NAA, naphthalene acetic acid; MS, Murashige and Skoog (1962); MT, Murashige and Tucker (1969); N6, Chu (1978); Nitsch, Nitsch (1951).

propagation (Wakasa, 1979, 1989; Smith and Drew, 1990). Spiny variants have also been observed in micropropagated 'Red Spanish' (Liu *et al*., 1987). A range of other somaclonal variants have been described by Wakasa (1989), including variants for leaf colour, leaf shape, wax, foliage density and abnormal phyllotaxy. Spininess and dense-foliage variants were attributed to chimeras at the donor-plant level. However, most of the other variations were attributed to regeneration of plants from callus cultures, especially undifferentiated callus derived from the syncarp. Further studies of this nature are needed to establish the explant sources and culture conditions required to minimize somaclonal variation during micropropagation and transformation.

Smith (1988) and Damasco *et al*. (1998) outlined a number of strategies for minimizing somaclonal variation in micropropagated bananas, and central to these approaches were regular initiations of cultures while providing limits to the number of plants multiplied from a single explant. While no data exist on this aspect in pineapple, commercial tissue-culture laboratories usually limit multiplication to 300–1000 plants per explant. Roguing of off-types, particularly during nursery establishment, is also essential to reduce the percentage of off-types reaching the grower. Many of the somaclonal variants recorded by Wakasa (1989) would lend themselves to easy identification and roguing while the plants are quite small. Other less obvious variants, such as those that produce small, malformed or cracked fruit, require a fruiting cycle for identification. It is particularly important to grow all plants arising from tissue culture through a cycle of fruiting to enable roguing of all somaclonal variants.

In vitro germplasm conservation

Advancements in breeding and genetic engineering require that the genetic diversity of pineapples and their close relatives not only be preserved but be put to use for pineapple improvement. While tissue culture techniques offer the opportunity for rapid propagation, they also offer the convenience of medium- and long-term storage of germplasm and facilitate its safe distribution.

Lower temperatures (16–20°C, as opposed to 25–28°C for normal micropropagation) have been used successfully to extend subculture times for up to 4 years (Sugimoto *et al*., 1991). Zee and Munekata (1992) found that reducing the nutrient salts of the MS medium to one-fourth was successful for medium-term (12 months), low-input maintenance of pineapple cultures. For the long term, cryopreservation offers the best solution, as the processes leading to somaclonal variation during cell division are halted. Gonzalez-Arnao *et al*. (1998) obtained the first positive results in pineapple. Optimal conditions included a 2-day preculture of apices on a semisolid MS medium with 0.3 M sucrose, loading treatment for 25 min with a cryoprotective solution containing glycerol (1 M) and sucrose (0.75 M) and dehydration with a vitrification solution (30% (w/v) glycerol + 15% (w/v) DMSO + 0.4 M sucrose) at 0°C for 7 h before immersion in liquid nitrogen.

Anther and Ovule Culture

There is some interest in the development of haploid cultivars as a first step to circumvent the heterozygosity observed in segregating seedling populations. There is doubt whether the development of doubled haploids is likely to be a useful strategy, and other approaches, such as those involving some level of inbreeding, may be better. To date, limited success has been achieved with ovule culture, but anther culture appears more difficult (Benega *et al*., 1996).

Protoplast isolation and fusion

Like anther and ovule culture, there is some doubt whether the development of techniques for protoplast isolation and fusion are likely to be worthwhile in pineapple. Protoplasts have been used in some monocot species for transformation, but there are inherent problems associated with the use of

protoplasts and other approaches appear more applicable in pineapple. Protoplast fusion is sometimes used where parent incompatibility prevents hybridization by conventional means. This approach, however, will result in the development of tetraploid lines. Tetraploid pineapple cultivars studied to date have been inferior types (Collins and Kerns, 1947). Nevertheless, protoplasts of the cultivar 'Perolera' have been successfully isolated (Guedes *et al*., 1996), but plant regeneration was not achieved.

Genetic Engineering

The pineapple industry around the world is unique in its almost total reliance on a single cultivar. This industry, through its consistent use of a single cultivar from the birth of pineapple processing, has virtually fixed the identity of canned pineapple as 'Smooth Cayenne'. New cultivars for this market would need to be almost identical to 'Smooth Cayenne' in production, processing and organoleptic qualities. Improvements to this cultivar would therefore be difficult using conventional hybridization techniques. Genetic engineering, however, would have tremendous application for making small targeted changes without changing the integrity of the cultivar we know as 'Smooth Cayenne'.

To successfully genetically engineer pineapple, genes of interest first have to be identified and sequenced and a complementary DNA (cDNA) clone generated. A plasmid construct, including promoter, terminator regions, gene of interest and a selectable marker gene, can then be designed and constructed. Transformation techniques are then employed to introduce the new gene sequence into cells of the chosen cultivar.

Promoters

Promoters are segments of DNA that drive the expression of the new gene sequence (transgene) and they may or may not be tissue-specific. Early work indicates that promoter elements and constructs developed for use in other species can be adapted for use in pineapple. The maize ubiquitin (*Ubi-1*) and the cauliflower mosaic virus 35S (CaMV35S) promoters have been shown to function well in transient assays in pineapple fruit, leaves and callus (Graham *et al*., 1998). The transformation technique developed by DNA Plant Technology Inc. (DNAP) in the USA also utilizes these two most commonly used promoters (Firoozabady and Gutterson, 1998). However, confirmation of the genuine utility of these promoters in transgenic pineapple will await the generation and analysis of many stably transformed lines. Similarly, for driving expression of the *npt*II selectable marker gene, both the *Ubi-1* and CaMV35S promoters, and promoters derived from segments of the subclover stunt circovirus, have been used successfully to create stably transformed plants (Graham *et al*., 1998).

Transformation

Transformation techniques, using methods such as infection with *Agrobacterium*, electroporation or biolistics, enable us to introduce 'engineered' genes into plant cells. The *Agrobacterium* co-cultivation technique is based on the infective activity of the bacteria to introduce the recombinant DNA into the plant cells and thus act as a natural vector. *Agrobacterium* co-cultivation was conventionally the transformation method used for dicots. Monocots were found not to be susceptible to *Agrobacterium* infection in early studies, but more recent studies have indicated that many are and that *Agrobacterium* can be successfully employed for pineapple transformation. Other transformation methods employed for monocots include the introduction of novel genes into plant protoplasts (Hauptmann *et al*., 1987; Rathus and Birch, 1992). However, protoplasts are easily damaged and cultures do not always grow into morphogenic callus, to produce transgenic plant material. Another more successful transformation technique is biolistics, in which recombinant DNA coated on to gold or tungsten particles is propelled under gas pressure in a vacuum chamber into the plant cells. However, with this method multiple copies of the DNA can become incorporated

and there is less control over the precise location of the inserted DNA in the plant genome.

The transformation techniques that have achieved the most success to date are the direct introduction of transgenes by microprojectile bombardment (biolistics) and the indirect method by co-cultivation using an *Agrobacterium* vector. Both methods have been applied to pineapple; however, commercialization and patenting issues have in the past prevented the results of the work from being published widely. Nan *et al.* (1996) reported the use of the biolistics technique on liquid embryogenic protocorm cultures, obtaining low levels of transgenic material. Graham *et al.* (1998) have successfully employed the biolistics technique to callus cultures, achieving an average of 1% transformation efficiency. On the other hand, Firoozabady and Gutterson (1998) have produced transgenic pineapples using the *Agrobacterium*-mediated technique on embryogenic callus cultures, while Isidron *et al.* (1998) have reported GUS positive activity using a similar system. Graham *et al.* (1998) have successfully employed *Agrobacterium* co-cultivation to 'Smooth Cayenne' pineapple leaf bases, resulting in the production of organogenic callus cultures and transgenic plants, with transformation efficiency levels of about 2%.

All methods require a good and reliable regeneration system (Rangan, 1982) to produce transgenic plants from transformed cells. Using Wakasa's (1989) recipe for 'Smooth Cayenne', Graham *et al.* (1998) initiated callus on 90% of excised leaf bases from well-developed micropropagated shoots within 3–4 weeks. Callus was maintained on the same medium for proliferation, producing different types of callus, very similar to those described by Taylor *et al.* (1992) for sugar cane. The majority of callus consisted of compact, hard, globular, yellow-green, smooth-surfaced structures. This type of callus was regenerated through organogenesis. To a much lesser extent the second (yellow and friable) and third type (soft, mucilaginous, grey-yellow) of callus was also produced. Only the first type of callus is believed to be morphogenic.

Traits that have been targeted for improvement in 'Smooth Cayenne' using genetic engineering include nematode resistance, pineapple mealy-bug wilt-virus resistance, flowering and fruit-ripening control and black heart resistance (Botella *et al.*, 1998; Graham *et al.*, 1998; Rohrbach *et al.*, 1998; Sanewski *et al.*, 1999).

In vitro selection procedures

In vitro selection of transgenic material is achieved by cointroducing a resistance gene with the gene of interest. The most commonly used selective genes are those conferring resistance to an antibiotic (Dekeyser *et al.*, 1989; Caplan *et al.*, 1992) or herbicide (Vasil *et al.*, 1992; Cole, 1994; Dennehey *et al.*, 1994). The transgenic material can be screened *in vitro* by survival on a culture medium containing the selective agent. Graham *et al.* (1998) found that geneticin at 50 μg ml^{-1} and hygromycin at 20 μg ml^{-1} were useful selective agents, but not kanamycin, even at concentrations as high as 500 μg ml^{-1}.

The choice of selective gene can have substantial consequences on the consumer acceptance of the final product. Consideration should be given to the likely concerns of the public when choosing selective genes.

Evaluation of transgenics

Incorporation of the introduced gene in putative transgenic material can be determined *in vitro* by polymerase chain reaction (PCR) analysis, in which specifically designed primers can detect the presence or absence of the novel gene in the plant tissue. This early evidence can identify 'escapes' or non-cotransformed individuals when cointroduction of the novel gene and the selective gene was employed.

To confirm insertion of the novel and selectable marker genes in the transgenic lines, the PCR needs to be followed up by Southern blot analysis, which detects the actual presence of the introduced DNA fragment after DNA extraction from the tissue. This technique will also give an indication of copy numbers inserted in the genome.

Intellectual property and licensing

Intellectual property (IP) is another important issue in the application of genetic engineering for pineapple improvement. Many of the enabling technologies are patented and cannot be used commercially without licence agreements. The *Agrobacterium* co-cultivation technique for pineapples has been patented, although patents tend to be written quite specifically to cover particular sections of the protocol and are country-specific with an expiry date. The promoters *Ubi*-1 and 35S are also patented. IP issues may even impede the design of a certain plasmid construct, e.g. patents on using an antisense or co-suppression construct design.

It is generally prudent to be aware of all IP before commencing work that may ultimately infringe the rights of others when commercialized. The issues associated with this are very complex, but must be resolved before transgenic pineapples are grown commercially.

Environmental and health risk assessment

Biosafety and public acceptance of transgenic crops represent at least two other factors that must be considered before commercialization. The former does not seem to be a major issue with pineapple, primarily because there is little chance of gene escape into the environment.

Public acceptance is currently a major issue with all transgenic crops. The perceived safety of transgenic foods and the ownership of genetic material are at the centre of these concerns. It is difficult to anticipate changes in acceptance, but advances in transformation techniques, such as the development of selectable markers to replace antibiotic resistance markers and the use of the technology for more consumer-orientated product improvements might improve acceptance. Irrespective of changes in acceptance, it is evident that food-labelling laws in many countries will demand the identification of genetically modified contents. These laws will then require identification and segregation of fields of genetically modified plants. It is important for the pineapple industry to embrace protocols at this early stage to enable identification and segregation of genetically modified plants and thus ensure consumer confidence.

Molecular Markers

Genetic classification in the genus *Ananas* was originally based on quantitative, morphological (Smith and Downs, 1979) and qualitative variables. Such classifications were initially re-evaluated using enzymatic markers (isozyme analysis). In more recent years, several DNA-based marker techniques, such as random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP) analysis, have been used. There are no reports of these techniques being used to directly assist hybridization strategies in pineapple.

Enzymatic markers

Isozymes were used in the first systematic studies of the pineapple by Garcia (1989), with eight enzyme systems involving ten loci, and by Aradhya *et al.* (1994), with six systems involving seven loci. They found a high heterozygosity and polymorphism in *A. comosus*, with most variation between the botanical varieties. In some cases, clones from the same cultivar showed differences in some systems. DeWald *et al.* (1992) tested eight enzymatic systems and found variable, well-resolved banding patterns for peroxidase (PER) and phosphoglucomutase (PGM). Their study, as well as that of Laempet and Saghuanrungsirikul (1998), also showed incomplete correspondence between cultivars and zymotypes, and hence some unreliability for cultivar identification. Pérez *et al.* (1995) applied the isozyme analysis technique to detect mutant lines developed by cobalt-60 (^{60}Co) gamma irradiation of callus, while Arias Valdes *et al.* (1998) used the technique to evaluate ploidy levels.

DNA markers

DNA-based markers are more sensitive than enzymatic markers and are widely used for cultivar identification, for gene isolation and, perhaps most significantly, to monitor the segregation of chromosome regions known to be involved in controlling agronomic characters (quantitative trait loci (QTLs)). In pineapple this technique has been used mainly to classify cultivars.

Ruas *et al.* (1995) used RAPD analysis to estimate the relationships among four varieties. Polymorphism was observed in agreement with classification based on morphological characters. Noyer *et al.* (1996) used RFLP analysis on ribosomal RNA and found the genus *Ananas* to be very homogeneous. The results suggested variation within *A. ananassoides* that could constitute the origin of *A. comosus*. The most comprehensive study has been by Duval *et al.* (1998). Their results were consistent with the classification of pineapples in one genus and two species (see Coppens d'Eeckenbrugge and Leal, Chapter 2, this volume). This study indicated that variability was generally continuous between current species, and *A. comosus* and *A. ananassoides* appear to be the most diverse groups.

In the long term, spectacular advances in mapping technologies and the study of whole genomes can be confidently predicted. A major European Union (EU)-funded project in this field aims at characterization and gene mapping for linking markers to morphological traits and disease resistance (Coppens d'Eeckenbrugge *et al.*, 1998).

Conclusion

Pineapple tissue culture will continue to play a valuable role in clonal propagation schemes. Genetic engineering will also become an established method for pineapple improvement, particularly in cultivars, such as 'Smooth Cayenne', that do not lend themselves readily to improvement by conventional breeding strategies. The main obstacle to their widespread adoption will be somaclonal variation. Reliable methods will be required for the control and detection of deleterious off-types produced during *in vitro* culture, and certainly before plants are grown in the field.

Molecular markers have become powerful tools in pineapple taxonomy and will assist with more precise identification and classification. They will also become extremely useful in hybridization programmes for the selection of parent combinations containing the most important traits, thus reducing the number of generations required.

At the annual meeting of the Biotechnology Industry Organization in June 1998, Charles Shapiro, the Chairman of Monsanto Agricultural Company, compared the stage of development of the biotechnology industry today to that of the information technology industry in 1973. Although computers had been known since the 1940s, most of the rapid advances that have made the information technology industry what it is today have taken place in the past 25 years. If that is truly where the biotechnology industry is today, then today may be just the beginning and the next 25 years could be the real biotechnology revolution.

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5 Crop Environment, Plant Growth and Physiology

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Introduction

Pineapple, a crop native to the tropical Americas, is currently grown commercially over a wide range of latitudes from approximately 30°N in the northern hemisphere (30°45′N in India (Hayes, 1960) and 28°30′ in the Canary Islands (Galan Sauco *et al*., 1988b)) to 33°58′S in South Africa (Bartholomew and Kadzimin, 1977; Table 5.1). Pineapple seldom requires less than 12 months from planting to harvest and more commonly 18–24 months, or even as much as 36 months in cool subtropical environments. The induction of flowering of pineapple is almost universally initiated with a growth regulator (see Hepton, Chapter 6, and Bartholomew *et al*., Chapter 8, this volume), which has made large-scale production of pineapple possible in areas where flowering would otherwise be too erratic for commercial production. Further, in many areas where the crop is grown, fruiting may be forced in most or all months of the year, so it is common for both vegetative and reproductive growth to occur during both warm and cool seasons.

Production at the more extreme latitudes is mainly restricted to areas where the climate is moderated by the ocean, as the crop will not tolerate freezing temperatures. One of the main features of pineapple is its adaptation to areas of low rainfall, although productivity is reduced in drought conditions. This is partly due to the fact that pineapple, as with most *Bromeliaceae*, has the crassulacean acid metabolism (CAM) photosynthetic pathway. This specificity of pineapples is unique among plants widely cultivated for commercial purposes.

Pineapple-based cropping systems throughout the world vary from gathering fruit from wild plants under tree cover, as in some areas of Brazil, and intercropping systems that include pineapple and a wide variety of tree and herbaceous crops (Lee, 1972; Nair, 1977; Bavappa *et al*., 1986; Darwis, 1990; Oladokun, 1990; Cai and Zheng, 1991) to highly intensive monoculture cropping systems on thousands of hectares, as is the case in Hawaii, Indonesia, the Philippines and Thailand. As a result, yields are extremely variable and can range from 30 to more than 100 Mt ha^{-1}, depending on the length of the crop cycle, environmental conditions, cultural practices and the pineapple variety being grown (Py *et al*., 1987). High productivity of pineapple depends on successfully managing controllable factors, such as water and nutrient supply and pests and diseases (see Hepton, Chapter 6, and Rohrbach and Johnson, Chapter 9, this volume). Environmental factors, such as temperature, irradiance and rainfall, interacting with the plant's CAM and the unique morphological and anatomical

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Table 5.1. Temperature and length of crop cycle at various pineapple-growing areas in the world.

Location	Latitude	Elevation (m)	Temperature (°C)			Months to plant crop		F to H (days)	Reference
			Average	Max.	Min.	Force (F)	Harvest (H)		
Nyombe, Cameroon	4.5°N	70				6	11		Gaillard, 1970
Mt Cameroun, Cameroon		0	26.2	30.2	22.3	10		150	Aubert *et al.*, 1973
		550	22.6	27.6	17.7	10		180	
		1000	19.9	25.0	14.9	10		210	
Johore, Malaysia	1°22′N	5	26.9	35.0	18.9				Wee, 1969
Pekan Nenas, Malaysia						10	15–17*		Wee, 1969
Abidjan, Côte d'Ivoire	5°N	25	26.6	30.9	22.3	8–11*	13–15*	156–166*	Lacoeuilhe, 1978
Bangkok, Thailand				32.2	23.3				Neild and Boshell, 1976
Ivoloina, Madagascar	18°03′S	20	23.8	28.0	19.6	8–10*		144–221*	Moreau and Moreuil, 1976
Buenos Aires, Costa Rica	9°10′N		23.0	32.0	19.9	13	20		Romero *et al.*, 1973
Cali, Colombia				31.1	18.1	16			Neild and Boshell, 1976
Fort de France, Martinique	14°30′N	20				10			Lacoeuilhe and Gicquiaux, 1971
		60				10			
		350				11			
Foulaya, Guinée	10°N	400	24.7	30.7	18.7	13	19	180	Py *et al.*, 1957
Sape, Brazil	7°5′S	124	25.9	31.2	20.6				Giacomelli and Py, 1982
Coracao de Maria, Brazil	12°14′S	267	23.6	30.0	17.3				
Serra, Brazil	21°S	76	24.1	27.6	20.6				
Lagoa Santa, Brazil	19°38′S	778	21.4	26.5	16.3				
Monte Alegre, Brazil	18°52′S	756	22.3	29.1	15.6				
Osorio, Brazil	29°55′S	38	19.6	23.8	15.4				
Rio Pedras, Puerto Rico	18°23′N	23	24.8						Pico, 1974
Rock Hampton, Australia	23°26′S	11.3	22.7	27.2	16.7				Bartholomew and Kadzimin, 1977
Brisbane, Australia	27°28′S	42	20.5	25.5	9.5				Tkatchenko, 1947
Nambour, Australia	26°38′S			29–20.5†	19–6.0†			203–301*	Wassman, 1990
Yeppoon, Australia	23°6′S			30–23.0†	21–11.0†				

Wahiawa, Hawaii	21°20′N	200	22.6	30.1	14.3	14	23		Bartholomew and Kadzimin, 1977
Kunia, Hawaii		216		25–19.5†		9		175–223*	Fleisch, 1988
Maui, Hawaii		91	23.5	27.9	19.1	12		181–207*	Bartholomew and Malézieux, 1994
		300	21.8	25.7	17.9	12		195–213*	
		792	19.5	24.3	14.7	12		230–255*	
Touliu, Taiwan	23°44′N	48				16	23		Su, 1969
Karenko, Taiwan	23°58′N	19	22.2	27.1	17.3				Tkatchenko, 1947
Thika, Kenya	1°01′S	1463	20.5	> 35	5.5		22–30*		Lebedev, 1970
Kiamba, Kenya	1°12′S	1731	19.0						
Tenerife, Canary Islands	28°N	50	19.5			9–15	16–24*	210–270*	Galan Sauco *et al.*, 1988a, b
		150	21.1						
		475	15.8						
Zululand, South Africa	28°S						18‡	210–240*‡	Lacoeuilhe and Sarah, 1990
East London, South Africa	33°02′S	125	18.6	22.8	14.4		24–36*		Strauss, 1960; Bouffin, 1991
Port Elizabeth, South Africa	33°58′S	55	17.2	21.2	13.3				Tkatchenko, 1947
Malkerns, Swaziland	26°30′S		16.8	28.0	4.0	22	32		Dodson, 1968

*Range for two or more plantings in different seasons.
†Range of the maximum and minimum mean monthly air temperature.
‡Clone of the Queen group.

features of pineapple ultimately determine productivity within a given environment.

Carbon Assimilation and Water Use

Carbon fixation via the CAM photosynthetic pathway

Three main types of photosynthetic pathway exist in higher plants. In the C3 type, the most widely distributed, CO_2 fixation catalysed by the enzyme ribulosebisphosphate carboxylase/oxygenase (Rubisco) results in the synthesis of a three-carbon acid. In C4 plants – for crops, mainly *Graminaceae* of tropical origin – CO_2 is initially fixed by the enzyme phosphoenolpyruvate carboxylase (PEP-Case) into a four-carbon acid in leaf mesophyll cells. The four-carbon acid is then transported to adjacent bundle-sheath cells where decarboxylation liberates CO_2, which is fixed by Rubisco. This decarboxylation is accompanied by an increase in the intracellular CO_2 concentration, which stimulates photosynthesis by inhibiting photorespiration and increases water-use efficiency (WUE) (Hatch, 1975; Wong *et al*., 1979). A third category of plants, which includes pineapple, also fix CO_2 via PEP-Case and Rubisco. However, in these plants, a temporal separation occurs between the two carboxylation steps. Nocturnal fixation of CO_2 occurs via PEP-Case, and the C4 acids synthesized, mainly malic, are stored in the vacuole. The following day, decarboxylation of malate liberates CO_2, which is fixed by Rubisco. This type of photosynthesis, which results in large daily variations in the concentration of malate and which is found in species of the *Crassulaceae*, is termed crassulacean acid metabolism (CAM). The main feature of CAM plants is their high WUE. Malate decarboxylation during the day is associated with an increase in the internal CO_2 concentration and a subsequent decrease in the stomatal conductance, which reduces external CO_2 uptake and transpiration (for reviews, see Kluge and Ting, 1978; Osmond, 1978; Winter, 1985). Pineapple is the most important crop species exhibiting CAM.

Photosynthetic rhythm in CAM plants and in pineapple

Rhythmic patterns of net CO_2 exchange are well known in CAM plants, while photosynthetic O_2 evolution is less well documented. The diel rhythm of CO_2 fixation and O_2 evolution of an attached pineapple 'D' leaf (Fig. 5.1) displays the typical four-phase pattern of net CO_2 exchange in CAM plants described by Osmond (1978).

- Phase I corresponds to nocturnal carboxylation of phosphoenolpyruvate (PEP) via PEP-Case to form oxaloacetate (OAA). OAA is reduced to malate and stored in the chlorenchyma cell vacuoles. The internal CO_2 partial pressure remains low during this time and stomatal conductance is high. The substrate for PEP production in pineapple is mainly soluble sugars (Borland and Griffiths, 1989; Carnal and Black, 1989). In terms of balance, internal CO_2 from respiration is also fixed via PEP-Case and contributes to the malate pool. Night O_2 uptake data (Fig. 5.1) indicate that, in a 'D' leaf, CO_2 produced by respiration represents approximately 10% of the total CO_2 fixed into malate at night (Côte, 1988). Night net CO_2 fixation in pineapple generally accounts for at least two-thirds of the total net fixation of the day–night period (Neales *et al*., 1980; Bartholomew, 1982; Nose *et al*., 1986; Côte, 1988). Reported values for 21 studies in controlled environments with various photo- and thermoperiods and light levels ranged from 40 to 100%, with a mean of 80 $\pm$ 17% (Bartholomew and Malézieux, 1994). The proportion of CO_2 fixed nocturnally by pineapple plants propagated *in vitro* shifted progressively from 0 to 70% as plant fresh weight increased from 1 to 300 g (Côte *et al*., 1993). These observations support the idea that pineapple is an obligate CAM plant.
- Phase II, at the beginning of the day, corresponds to the transition from net CO_2 fixation via PEP-Case to CO_2 fixation via Rubisco. Malate decarboxylation begins during this phase, the internal CO_2 partial pressure gradually increases and stomatal

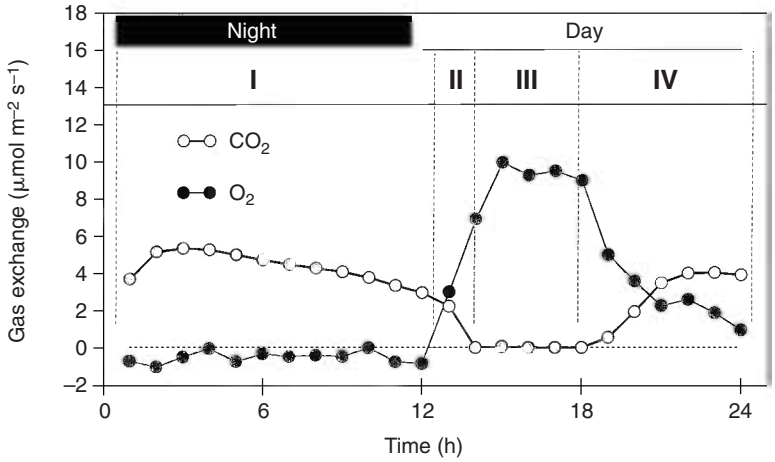

Fig. 5.1. Net CO_2 and O_2 exchange rates of an attached 'Smooth Cayenne' pineapple 'D' leaf throughout a night/day cycle (Côte, 1988). Both CO_2 fixation and O_2 evolution are indicated as positive values. Positive values for O_2 evolution during the day result from photosynthesis, while negative values during the night indicate O_2 uptake due to respiration. The four phases of the CAM cycle as defined by Osmond (1978) are indicated at the top of the figure. Environmental conditions include: photosynthetic photon flux density, 400 μmol m^{-2} s^{-1}; photoperiod, 12 h night/12 h day; night/day temperature 22°C/26°C. Data are the average for 4 consecutive days.

conductance declines. The overall contribution to carbon gain is small during phase II and was 1–3% of the total day–night net CO_2 uptake by pineapple plants maintained in controlled conditions (Fig. 5.1).

- Phase III is a period when net CO_2 fixation is negligible for up to 5 h, while CO_2 generated by malate decarboxylation is fixed via Rubisco. The internal CO_2 partial pressure rises well above atmospheric levels, because the rate of malate decarboxylation exceeds the rate of internal CO_2 fixation via Rubisco. Net CO_2 release sometimes occurs during phase III. This high internal CO_2 partial pressure stimulates photosynthesis and results in the low stomatal conductance, which limits transpiration during this phase. Although net CO_2 uptake is nil during phase III, the maximum rate of photosynthetic carbon reduction via Rubisco occurs during this phase. Based on the assumption that 1.0 mol O_2 is evolved for every mol CO_2 reduced (Kaplan and Björkman, 1980), the rate of CO_2 fixation via Rubisco during phase III, deduced from the rate of O_2 evolution during this phase, could be 1.3- to six-fold higher than the maximum rate of net CO_2 fixation achieved by pineapple during the light period (Côte, 1988). In the data of Fig. 5.1, it is 2.4 times higher.
- Phase IV begins when the malate pool becomes depleted, the internal CO_2 partial pressure declines, stomatal conductance increases and net external CO_2 uptake resumes for the last hours of the day. In pineapple, this fixation generally amounts to 15–25% of the total net CO_2 uptake (Fig. 5.1). Early in the phase, there is a progressive shift from fixation of internally generated CO_2 towards external net CO_2 uptake. Following the assumption that 1.0 mol O_2 is evolved per mole of CO_2 fixed, it was estimated that only 60–80% of the total CO_2 fixed during the night by a pineapple plant was reassimilated via Rubisco when net CO_2 uptake resumed in phase IV (Côte *et al.*, 1989). A value of 75% can be deduced from Fig. 5.1. PEP-Case has been reported to be active during late phase IV in CAM plants (Kluge, 1969; Kluge *et al.*, 1982) and measurement of malate concentration

also suggested that CO_2 uptake via PEP-Case occurs in pineapple during late phase IV (Black *et al.*, 1982; Kenyon *et al.*, 1985). The O_2 and CO_2 gas-exchange data suggest that CO_2 fixation via PEP-Case during phase IV represents 3–15% of the nocturnal net CO_2 fixed by pineapple (Côte, 1988; Côte *et al.*, 1989).

Gas exchange measured under controlled conditions (Fig. 5.2) is atypical of what occurs in the field, where stochastic, rather than steady-state, environmental conditions prevail. Diurnal changes in weather probably influence to some extent both the duration and the intensity of the four phases of CAM. While extrapolation of results obtained in controlled conditions to plants in natural environments must be done carefully, *in situ* measurement of stomatal conductance and leaf titratable acidity confirm the general conclusions derived from studies in controlled environments.

Photosynthetic rate in pineapple

In CAM plants, both net CO_2 uptake and malate-decarboxylation-dependent CO_2 assimilation via Rubisco during phase III have to be considered to evaluate the photosynthetic rate. Net CO_2 fixation in the light (phase IV) ranged from 0.13 to 6.3 μmol m^{-2} s^{-1} for pineapple plants or 'D' leaves maintained in various conditions (Connelly, 1972; Neales *et al.*, 1980; Sale and Neales, 1980; Côte, 1988; Bartholomew and Malézieux, 1994). Night net CO_2-fixation values reported by the same authors ranged from 0.13 to 2.5 μmol m^{-2} s^{-1}, while others reported values as high as 5.0 to 7.8 μmol m^{-2} s^{-1} (Côte, 1988; Borland and Griffiths, 1989; Fig 5.1). It can be deduced from photosynthetic O_2 evolution that CO_2 reduction via Rubisco never achieves a steady state in pineapple (Côte, 1988; Côte *et al.*, 1989; Fig. 5.1). Data for O_2 evolution from a pineapple 'D' leaf also show that the CO_2 assimilation rate during

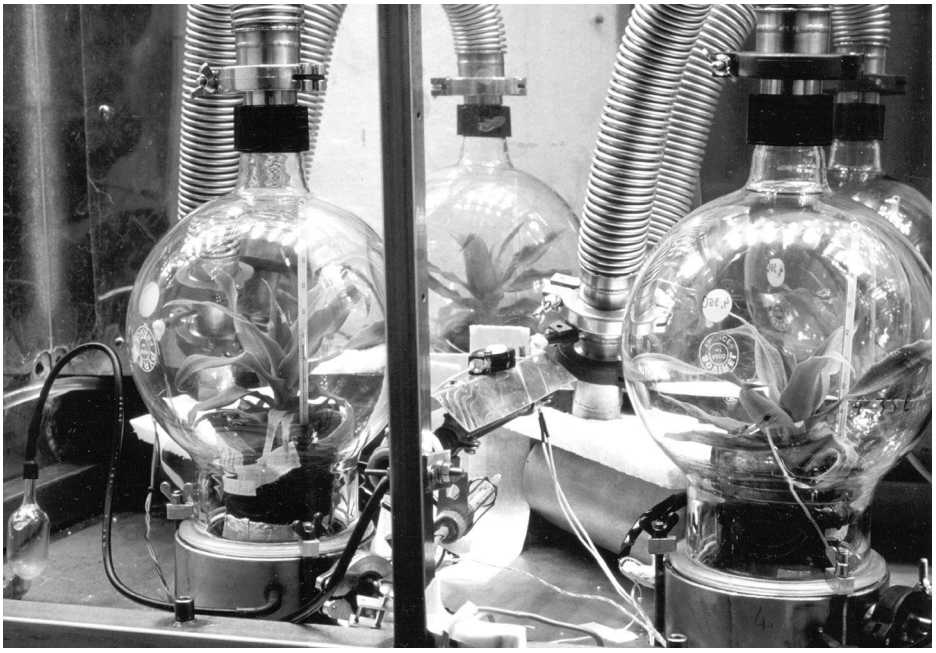

Fig. 5.2. Controlled-environment chambers used for gas-exchange measurements of 'Smooth Cayenne' pineapple plants from *in vitro* culture (Côte, 1988). Measurements were made in controlled atmosphere automatic growth chambers (CEA, Commissariat à l'Energie Atomique, 13108 St Paul-lez-Durance, France).

phase III reaches 9.9 μmol m^{-2} s^{-1}, a value much greater than the maximum value observed in phase IV (Côte, 1988) (Fig. 5.1).

The maximum CO_2-fixation rates for pineapple are comparable to those for other CAM plants, but are low compared with values of 8.33–25 μmol m^{-2} s^{-1} reported for C3 plants (Black, 1973). The low rates for pineapple relative to those of C3 plants is in part due to low leaf conductances to gas diffusion during phase IV (Côte, 1988), even when the stomata are wide open. The concentration of Rubisco per unit area of leaf could also be low relative to C3 plants (Winter *et al.*, 1982).

When CO_2 fixation by pineapple is expressed on a unit area of soil, fixation rates are also much lower than those for C3 plants. For example, in controlled conditions, a pineapple plant with a leaf area index (LAI) close to 4 fixed 20–25% of the CO_2 fixed by wheat (Côte *et al.*, 1993). However, dry-matter accumulation by a pineapple crop is high. Lacoeuilhe (1976) reported that pineapple accumulated 41 t of dry matter ha^{-1} during a crop cycle in Côte d'Ivoire. Bartholomew (1982) reported 62 t of dry matter ha^{-1} in 24 months in Hawaii. By way of comparison, dry-matter production of wheat was reported to be between 18 and 29 t ha^{-1} $year^{-1}$ (growing season), while that for sugar cane was 67 t ha^{-1} $year^{-1}$ (Loomis and Gerakis, 1975). The large dry-matter accumulation by pineapple is associated with a high LAI and the ability of leaves to maintain their photosynthetic capacity for long periods of time.

Water-use efficiency related to CAM in pineapple

Transpiration rhythm and transpiration rate in pineapple

In pineapple, the diel rhythms of stomatal conductance and transpiration are closely linked to the net CO_2-uptake rhythm (Neales *et al.*, 1968; Nose *et al.*, 1981; Bartholomew, 1982; Côte *et al.*, 1993; Fig. 5.3). The lowest rates of transpiration occurred during phases I, II and III and the highest during phase IV. WUE is two times greater during phase I than during phase IV and reaches a minimum during phase III (Fig. 5.3). The transpiration rates of pineapple ranged from 0.05 to 0.23 mmol m^{-2} s^{-1} (Ekern, 1965; Joshi *et al.*, 1965; Neales *et al.*, 1968; Nose *et al.*, 1981), while values for sunflower and tobacco were at least tenfold higher at about 3.1 mmol m^{-2} s^{-1} (Neales *et al.*, 1968). Transpiration by pineapple in the light in controlled conditions was only 4% of that of sunflower leaves grown in a similar environment (Neales *et al.*, 1968) and only 6% of that for wheat, and WUE was 3.3-fold greater (Côte *et al.*, 1993).

Leaf and canopy transpiration rates for pineapple are lower than those for most cultivated crops. At midday, there was no measurable water-vapour loss from a full pineapple canopy with an LAI of 7 (Ekern, 1965) and transpiration from pineapple plants in pots was 1.0 mm day^{-1} (monthly average) (Shiroma, 1971). The transpiration ratio (TR) (units water lost per unit dry-matter gain; kg kg^{-1}), a measure of the WUE, for pineapple was about 50 (Sideris and Krauss, 1955; Joshi *et al.*, 1965; Côte, 1988) to 116 (Neales *et al.*, 1968), while the range for C3 crops was 450–950 and that for C4 crops 250–350 (Kluge and Ting, 1978). A consequence of the low rate of water use is that the crop can sustain an LAI of greater than 7 (Malézieux, 1991; Zhang, 1992) over long periods under low-rainfall conditions (Ekern, 1965; Aubert, 1973).

Origins of the high water use efficiency related to CAM

Diffusion of water vapour from and CO_2 into plant leaves can be described by the equations:

$$\Delta W = r\,T \quad (1)$$

$$\Delta CO_2 = 1.6\,r\,P \quad (2)$$

where ΔW is the difference in water-vapour pressure between the stomatal cavity and the atmosphere, r is the resistance to water-vapour diffusion, T is the transpiration rate, ΔCO_2 is the difference in CO_2 partial pressure between the stomatal cavity and the atmosphere, 1.6 is the ratio of the diffusion

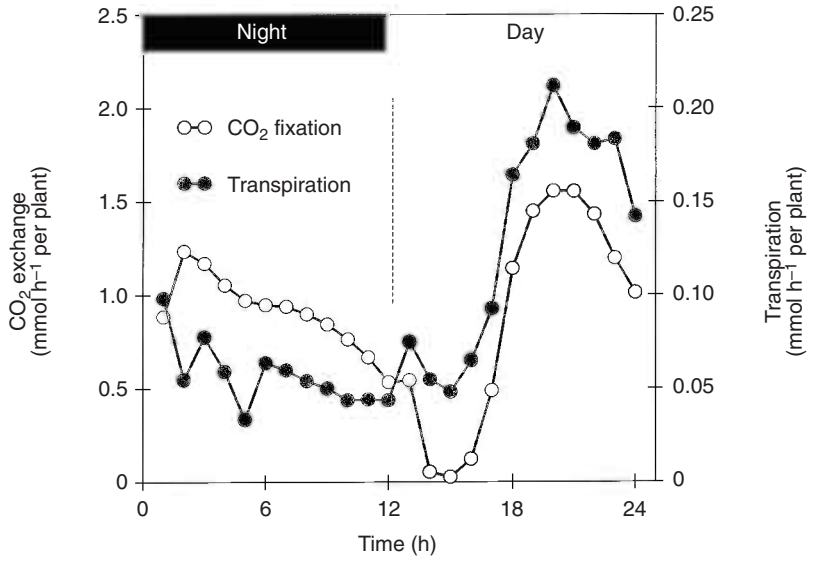

Fig. 5.3. Transpiration and net CO_2 exchange during a night/day cycle by a 'Smooth Cayenne' pineapple plant (Côte *et al.*, 1993). Environmental conditions include: photosynthetic photon flux density, 650 μmol m^{-2} s^{-1}; photoperiod, 12 h night/12 h day; night/day temperature, 22°C/28°C. The plant (fresh weight of aerial parts = 120 g) was obtained from *in vitro* culture. Data are the averages for 3 consecutive days.

coefficients for water vapour and CO_2 in air and P is the rate of net CO_2 fixation. Combining equations (1) and (2) gives:

$$T = 1.6 \times \Delta W \times P / \Delta CO_2 \quad (3)$$

The low transpiration rate in CAM plants is related to morphological and physiological adaptations that influence ΔW, P and ΔCO_2 of equation (3) to reduce T:

- Net CO_2 fixation (P) occurs mainly during the night when ΔW is low.
- During the day, when ΔW is high, malate decarboxylation increases the internal CO_2 concentration; consequently P is low or even zero.
- During phase IV ΔCO_2 is high (Côte *et al.*, 1993), reducing P and T.

The highest leaf conductances recorded for pineapple were about 3% of those observed for cotton (Neales *et al.*, 1968). This low conductance was attributed to a thick mesophyll, low stomatal frequency and sunken stomata located beneath multicelled trichomes (Bartholomew and Kadzimin, 1977).

Effects of environmental factors

Effects on photosynthesis

TEMPERATURE. The effects of temperature on photosynthesis of pineapple are complex and relatively few studies have been conducted. While the results of these studies are often not directly comparable, the general trends show that the intensity of CAM (phase I) is highest when the light/dark temperature differential is approximately 10°C and the night temperature is cool, about 20°C. These results are consistent with other observations that the optimum day/night temperature for growth also is about 30/20°C (Neild and Boshell, 1976; Bartholomew and Malézieux, 1994).

INCREASING NIGHT TEMPERATURE. At a given day temperature, an increase in the night temperature decreases night net CO_2 uptake (Connelly, 1972; Neales *et al.*, 1980; Zhu *et al.*, 1999), as well as the proportion of night fixation in a 24 h period (Connelly, 1972; Bartholomew, 1982; Bartholomew and Malézieux, 1994; Zhu *et al.*, 1999). Neales *et al.* (1980) and Zhu *et al.* (1999) reported a 50%

decrease in night uptake as the night temperature was increased from 20 to 25°C at a constant day temperature of 30°C. The decrease could be due in part to an increase in respiration-derived CO_2 fixation, but leaf titratable acidity also decreases (Min, 1995), indicating less total CO_2 dark fixation. Some studies show little or no change in net CO_2 uptake during the day with an increase in night temperature (Neales *et al.*, 1980; Zhu *et al.*, 1999), but Connelly (1972) reported a dramatic increase when night temperature increased from 15 to 30°C. It is at present not possible to resolve this discrepancy.

The relationship between net CO_2 fixation and dry-matter accumulation under various thermoperiods has also not been well studied. In one study, net CO_2 fixation of single attached leaves of plants grown for 8 months at 30/20°C was 1.6 times higher than that for leaves of comparable plants grown at 30/25°C, while whole-plant dry-matter accumulation was only 1.1 times higher in the cooler environment (Zhu *et al.*, 1997a). However, assimilation was measured only on 'D' leaves, while dry-matter accumulation reflects the contribution of leaves of all ages.

INCREASING DAY TEMPERATURE. At a given night temperature, the fraction of total CO_2 assimilated in a 24 h period that is fixed at night increases with increasing day temperature (Neales *et al.*, 1980; Bartholomew, 1982; Bartholomew and Malézieux, 1994; Zhu *et al.*, 1999). This increase is due primarily to a decrease in net CO_2 uptake in the day and to a lesser extent to an increase in net CO_2 uptake at night (Connelly, 1972; Neales *et al.*, 1980; Zhu *et al.*, 1999). For example, Zhu *et al.* (1999) reported that CO_2 uptake in the day decreased 50% as the day temperature was increased from 30/25°C to 35/25°C, while the increase in CO_2 uptake at night was much smaller. As a result, there was a 37% increase in the fraction of CO_2 fixed at night. The biochemical basis for the changes in CO_2 uptake with changing temperature is not well understood. It is hypothesized that the decline in net CO_2 uptake during phase IV with increasing day temperature is associated with increased respiration, but further studies are needed.

IRRADIANCE AND PHOTOPERIOD. Because CO_2 assimilation in CAM plants, including pineapple, occurs via the photosynthetic carbon reduction cycle, it is assumed that photosynthesis will increase with increasing irradiance, and the results of Shiroma (1977) and Nose *et al.* (1981, 1985, 1986) support this assumption. Nose *et al.* (1985, 1986) found that light saturation of pineapple plants occurred at a photosynthetic photon flux (PPF) of about 500 μmol m^{-2} s^{-1}. *In vitro*-grown plants maintained under continuous illumination also saturated at a PPF of 500 μmol m^{-2} s^{-1} (Côte, 1988). However, it is probable that variation in irradiance can alter the pattern of CO_2 fixation. For example, high irradiance decreases the duration of phase III and increases the duration of phase IV assimilation relative to what occurs at low irradiance (Nose *et al.*, 1986). This is because the rate of malate-decarboxylation-dependent CO_2 assimilation is more rapid during phase III (Sale and Neales, 1980), so the malate pool is depleted more rapidly. Increasing irradiance probably also increases the quantity of soluble sugar formed in leaves during phase III and IV. An increased supply of sugar available for the production of PEP, the substrate required for CO_2 fixation into malate at night, would increase the amount of CO_2 fixed into malate during phase I. Consistent with this hypothesis, an increase in irradiance during the day increased CO_2 fixation the following night (Nose *et al.*, 1981, 1985, 1986; Shiroma *et al.*, 1977), and leaf titratable acidity also increased with increasing irradiance (Sideris *et al.*, 1948; Connelly, 1969; Aubert, 1971; Sale and Neales, 1980). However, increases in night CO_2 fixation that follow an increase in irradiance generally are smaller than the increase in CO_2 assimilation in the light. Thus, the intensity of CAM tends to decrease as irradiance increases, at least until saturating levels are attained.

Little is known about the effect of photoperiod on pineapple photosynthesis. Nose *et al.* (1986) reported that as day length increased from 10 to 16 h, total uptake in the light increased while uptake at night decreased. However, expressed on an hourly basis, the increase in CO_2 uptake in the light

as day length increased was small, while the decrease at night was relatively large. A 40–50% reduction in CO_2 uptake at night can be deduced from the data of Nose *et al.* (1986) as photoperiod decreased from 16 to 8 h. In natural environments, e.g. Hawaii, the decrease in photoperiod from summer to winter is only 21%, while the decrease in irradiance is about 50%.

CO_2 CONCENTRATION. The effect of elevated CO_2 concentration on pineapple photosynthesis has not been well studied, but generally increases in response to elevated CO_2 have been observed. At a concentration of 1700 μmol mol^{-1} CO_2, net CO_2 fixation increased two- to threefold during phase IV (Côte, 1988) and a CO_2 concentration greater than 1000 μmol mol^{-1} was required to saturate photosynthesis in that phase. Saturation at such a high CO_2 level indicates that pineapple has a high resistance to CO_2 diffusion during phase IV.

Zhu *et al.* (1997b) reported that the dry mass of pineapple plants grown for 4 months at 730 μmol mol^{-1} CO_2 was 1.2 times higher than that of plants grown at ambient CO_2 (330 μmol mol^{-1}). In that study, 'D'-leaf titratable acidity at the end of phase I was more than 1.3 times greater for plants grown at elevated than at ambient CO_2. Net CO_2 uptake in phase I was also enhanced, but only where average temperature was above 25°C. Uptake of CO_2 during phase IV was also enhanced and the effect of enrichment was greater as the average temperature increased from 25 to 30°C (Zhu *et al.*, 1997b). Nocturnal CO_2 fixation has been reported to be insensitive to high CO_2 levels in other CAM plants, so the origin of these different responses is unknown. Further studies are required to understand the combined effect of thermoperiod regime and elevated CO_2 partial pressure on pineapple photosynthesis.

WATER STRESS. When CAM plants are subjected to drought, CO_2 fixation during phase IV soon ceases. If the period of water stress is extended, net CO_2 fixation ceases but CAM plants continue to refix respired CO_2, a phenomenon referred to as CAM idling (Kluge and Ting, 1978). Pineapple plants subjected to water deficit exhibit a similar response (Fig. 5.4). When well watered, CO_2 fixation during the day and night was normal, with 45% of the CO_2 being fixed at night. Depending on plant size and perhaps moisture supply, drought reduced CO_2 uptake in the light rapidly (Fig. 5.4) or relatively slowly (Zhu, 1996). With small plants, uptake in the day was nil after 4 days without water, while, for large plants, net uptake in the day by attached 'D' leaves ceased after about 15 days. For small plants (Fig. 5.4), transitory net CO_2 evolution occurred as the period of water stress lengthened. Nocturnal CO_2 fixation rate was not affected at the beginning of water stress, but decreased progressively as the duration of water stress lengthened (Fig. 5.4; Zhu, 1996). After rewatering, CO_2 uptake in both phase I and phase IV resumed rapidly (Fig. 5.4). The reduced sensitivity of night CO_2 uptake to water deficit, as compared with day CO_2 fixation, and the reversibility of the effects of water deficit in pineapple are consistent with observations for other CAM plants (Kluge and Ting, 1978).

Water deficit also alters the pattern of CO_2 assimilation. At the onset of water deficit, there was a transient stimulation of net CO_2 uptake at the beginning of the night period. As drought was prolonged, the maximum rate of CO_2 assimilation shifted progressively towards the end of the night period (Côte *et al.*, 1993; Zhu, 1996), and the shift was more marked at 25°C night temperature than at 20°C. Zhu (1996) also showed that the rate of decline of net CO_2 assimilation during drought was related to the day/night temperature regime. Fluctuations in leaf titratable acidity indicated that significant assimilation – about 35% of the maximum – still occurred after 70 days of drought at 30/20°C, while at warmer temperatures (35/25 and 30/25°C), titratable acidity was 20% or less of the maximum after only 40 days of drought. While pineapple is highly tolerant of drought, assimilation declines fairly rapidly with drought, and warm temperatures hasten the rate of decline.

Effects on plant water relations

Transpiration rate is closely related to net CO_2 uptake and to the differences in water-vapour pressure and CO_2 partial pressure

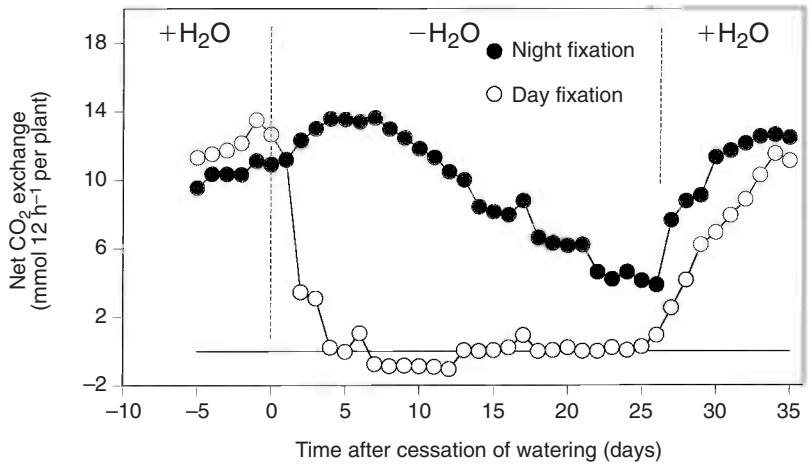

Fig. 5.4. Effect of water deficit on the daily photosynthetic CO_2 exchange by a 'Smooth Cayenne' pineapple plant (Côte *et al.*, 1993). The plant was placed on an inert culture support aluminium silicate). Watering with the nutrient solution was stopped on day 0 and was resumed on day 26. Environmental conditions include: photosynthetic photon flux density, 650 μmol m^{-2} s^{-1}; photoperiod, 12 h night/12 h day; night/day temperature, 22°C/28°C. The plant (fresh weight of aerial parts = 100 g) was obtained from *in vitro* culture.

between the stomatal cavity and the atmosphere (equation 3). Thus the effects of environmental factors on plant water relations are closely linked to those of environmental factors on photosynthesis (Côte, 1988; Zhu, 1996; Zhu *et al.*, 1997a).

TEMPERATURE. For pineapple held at a constant day temperature, daytime transpiration rates decreased as the night temperature increased, while transpiration rates at night remained constant (Yoder and Bartholomew, 1969a,b). These results are consistent with the results of CO_2 assimilation studies, which show that larger day/night temperature differentials decrease assimilation in the light. Mean values for WUE were higher when night temperatures were lowest (Zhu, 1996). For example, WUE at night was more than 1.3 times higher for pineapple plants maintained in a day/night temperature of 30/20°C compared with those maintained at 30/25°C. In the light, WUE was more than 1.5 times greater at 30/25 than at 35/25°C (Zhu, 1996).

Stomatal conductance (g_s) of pineapple is typically lowest during the day and highest at night, referred to as an inverted pattern of stomatal opening. However, in a 10/25°C day/night temperature regime, g_s was much higher during the day (51 mmol m^{-2} s^{-1}) than at night (8.1 mmol m^{-2} s^{-1}) (Neales *et al.*, 1980), reversing the typical inverted pattern of stomatal opening.

Few data on g_s are available under field conditions. In Côte d'Ivoire, g_s data indicated that the stomata opened earlier in the afternoon when the day/night temperature differential was 9°C than when it was 14°C (J.C. Combres, 1981, personal communication). Conversely, a dry wind, such as the Harmattan in West Africa, induced prolonged closing of the stomata, with opening occurring late in the night (Py *et al.*, 1987). Based on these data, we predict that consumptive use of water by pineapple would be higher in tropical environments, with high night temperatures and a small day/night temperature differential, than it would be in more subtropical environments, where larger day/night temperature differentials prevail.

IRRADIANCE. Because pineapple transpires little or not at all during the day, it is expected that irradiance would have a limited effect on transpiration. However, high irradiance tends to increase the rate and duration of CO_2 fixation during phase IV because the stomata open earlier in the afternoon. This

would be expected to increase transpiration during the day, and Nose *et al.* (1981) reported an increase in transpiration with increasing irradiance.

CO_2 CONCENTRATION. Zhu *et al.* (1999) reported a 1.1–1.2-fold increase in WUE during the night and a 2.3–2.7 fold increase in the day for pineapple plants grown at 700 μmol mol^{-1} CO_2 compared with those grown at 350 μmol mol^{-1}. Depending on the day/night temperature regime, the 24 h WUE was 1.3–1.6 times higher at 700 μmol mol^{-1} than at 350 μmol mol^{-1}. Zhu *et al.* (1999) clearly demonstrated that higher WUE was associated with a two- to threefold decrease in stomatal conductance during phases IV and I.

WATER STRESS. The patterns of g_s during the onset of water stress are similar to those of net CO_2 uptake. Zhu (1996) observed a rapid decrease in g_s for pineapple plants subjected to drought during phase IV and a somewhat slower decrease during phase I. After 15 days of drought, g_s was near zero during phase IV. In phase I, the time when g_s reached a maximum shifted from early in the light period to towards its end. In ambient CO_2, WUE decreased progressively as water stress progressed. However, plants maintained at 700 μmol mol^{-1} CO_2 exhibited a steady increase in WUE (Zhu, 1996). In a field study, J.C. Combres (1981, personal communication) observed that, after rainfall following a period of drought, the stomata open progressively earlier in the morning and in the afternoon in the following days.

Plant Growth and the Environment

Main characteristics of vegetative plant growth

Pineapple is grown from a variety of propagules (see Hepton, Chapter 6, this volume) but all develop in a similar manner. If conditions for growth are favourable after planting, root initiation begins, followed by the appearance of new leaves. Between planting and inflorescence initiation, growth occurs in the root, stem and leaf meristems. Pineapple varieties that have strong apical dominance, such as 'Smooth Cayenne', generally do not produce shoots from stem axillary buds prior to flower induction, and shoots are typically not produced by 'Smooth Cayenne' in warm tropical environments until after fruit harvest. 'Queen Victoria' (Maerere, 1997) and 'Red Spanish' have weaker apical dominance and may initiate shoots prior to flower induction, even in tropical environments.

Shoots of the same initial mass, whether suckers or crowns, have approximately the same leaf area despite quite large differences in leaf number and size. Crowns have numerous short leaves, while suckers have fewer but longer leaves. In an experiment in Côte d'Ivoire, the leaf appearance rate in the month after planting was 8 for crowns and 3 for suckers (Lacoeuilhe, 1976). Beyond 3 months, leaf emergence rate was similar for crowns and suckers. During the first few months of growth, leaves produced by suckers are longer and heavier than those produced by crowns. For planting material of similar size, leaf emergence rate and leaf size are similar within 3–5 months after planting (Py *et al.*, 1987).

Leaves

Leaves represent approximately 90% of aerial plant fresh weight during vegetative growth (Py, 1959). Leaves grow from the base, the maximum leaf length is reached several months after initiation and leaves of a wide range of sizes and ages are present on the plant at the same time (Fig. 5.5). The time from initiation to full elongation depends on temperature and is approximately 4 months in the nearly equatorial conditions of Côte d'Ivoire, but considerably longer in cooler environments. Sideris and Krauss (1936) separated pineapple leaves into categories based on their similarity in size and age. The 'D' group of leaves were the longest on the plant and had 'succulent–brittle' leaf bases. Over time it became common practice to apply the term 'D' to a single leaf, usually the tallest leaf on the plant. This 'D' leaf represents an easily identified standard leaf (Fig. 5.6) that is commonly used to index growth and evalu-

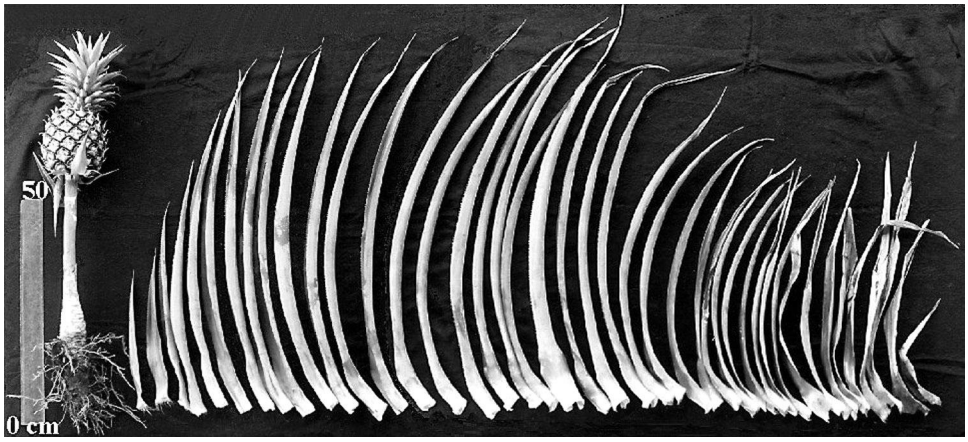

Fig. 5.5. Array of leaves present on a fruiting pineapple plant. The oldest leaves are to the right of the stem and its associated peduncle and fruit. (Photo of E. Malézieux.)

ate plant nutrient status. When growth is rapid, the tallest leaf is almost always nearly but not fully expanded (Py *et al.*, 1987). When growth is unrestricted by stress, the maximum length, width, and weight of individual leaves increase with each successive leaf until a maximum is reached (Fig. 5.5). Maximum leaf length may differ among pineapple varieties, but, for 'Smooth Cayenne', the maximum length can reach 100 cm and the maximum width can reach 7 cm (Py *et al.*, 1987). Total leaf area per plant can reach 2.2 m^2 for a plant having a fresh weight of 3.6 kg (Py, 1959). The LAI of a pineapple canopy can reach 12 at floral induction, although values of 6–8 are more common.

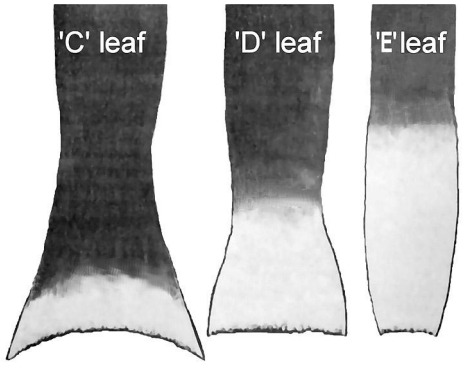

Fig. 5.6. The pineapple 'D' leaf is most accurately identified by the more or less parallel margins of the leaf base as contrasted with the flared base of the older 'C' leaf on the left and the tapered base of the young 'E' leaf on the right. For mineral-nutrient analysis, the middle one-third of the basal white tissue is sampled. (Modified from Nightingale, 1949.)

Roots

Few data are available on root growth. Though roots of 'Smooth Cayenne' pineapple can theoretically reach a length of 1.8 m and grow to a depth of 85 cm (Sideris and Krauss, 1934), the sensitivity of pineapple roots to soil compaction (Rafaillac *et al.*, 1978; Ikan, 1990) generally confines the root system to the tilled area (Ekern, 1965; Ikan, 1990; J.J. Lacoeuilhe and E. Malézieux, unpublished results). This restricted soil volume prospected by the roots can limit the amount of water available to the plant. After planting, crowns produce more roots than suckers (Py *et al.*, 1987). There is evidence that root growth decreases after flower induction and that maximum root mass is reached at anthesis.

Stem and axillary buds

Stem mass increases progressively after planting, with no unique morphological changes until reproductive development begins. Plants may accumulate starch reserves in the stem, but such accumulation varies with plant age and size and aerial

environment. Soon after floral induction occurs in 'Smooth Cayenne', axillary bud development usually begins, but active growth is highly dependent upon climatic conditions. Axillary shoot growth occurs during fruit development on relatively large but not on small 'Smooth Cayenne' plants in subtropical conditions, but only after fruit harvest in tropical environments having warm night temperatures. This may be related to the higher starch content of the stem in plants growing in subtropical conditions, where the night temperature is cooler and the day/night temperature differential is larger. The growth of one to a few suckers makes possible the production of one or more second fruits on the mother plant (ratoon crop) and these shoots are also used as propagules.

Morphological, anatomical and physiological features and adaptations to environmental conditions

Water use

Leaves are arranged spirally around the stem in a dense rosette pattern (see Coppens d'Eeckenbrugge and Leal, Chapter 2, this volume). This shape and orientation channel light rains and dew to the base of the plant, making a significant contribution to the water economy of the plant (Ekern, 1965, 1968).

Large trichomes completely cover both adaxial and abaxial leaf surfaces (Fig. 5.7), and a highly cutinized upper epidermis and a multicelled hypodermis are two significant morphological and anatomical features of pineapple leaves that contribute to the plant's water economy (Krauss, 1930, 1949; see Coppens d'Eeckenbrugge and Leal, Chapter 2, this volume). There are 30–35 trichomes mm^{-2} on the abaxial leaf surface (Aubert, 1973), which cover strips of stomata located in furrows between ridges devoid of stomata (Fig. 5.7). There are relatively few stomata per unit leaf area (70–85 mm^2) and the stomatal pore is small (Krauss, 1949; Bartholomew and Kadzimin, 1977).

The mature 'Smooth Cayenne' leaf cross-section can be up to 4 mm thick (Krauss, 1949), with approximately half the volume of the plant leaf occupied by a water-storage parenchyma. The balance of the leaf volume

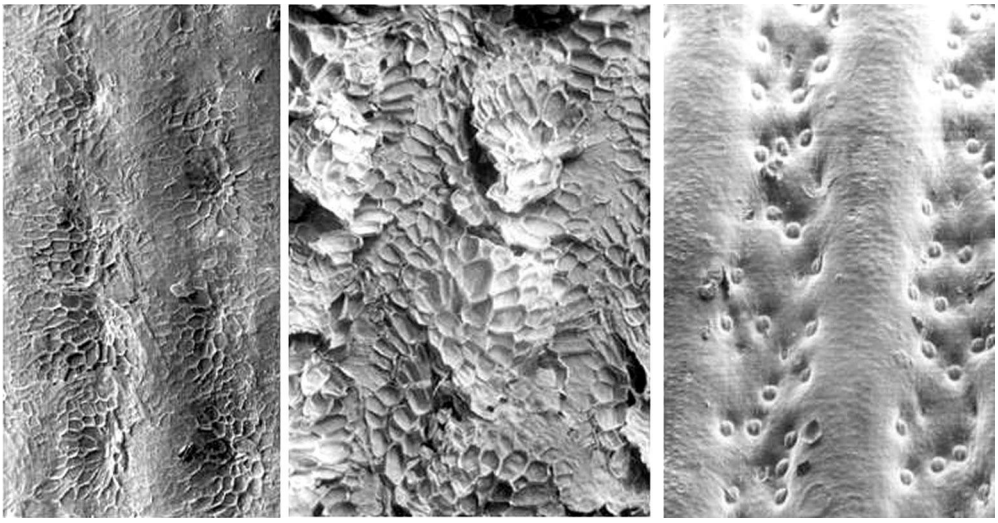

Fig. 5.7. Scanning electron micrographs (SEM) showing the large multicellular trichomes on the adaxial and abaxial surfaces of a 'Smooth Cayenne' pineapple leaf. Note that the trichomes are much more prominent on the abaxial surface. In the right-hand SEM, the trichomes have been removed from a section of the abaxial surface to show the rows of stomata located in furrows that parallel the longitudinal axis of the leaf. (Scanning electron micrographs of D. Bartholomew.)

is chlorenchyma. This water-storage parenchyma functions as a reservoir of water, which is utilized during periods of drought. The depleted tissue is replenished after adequate rain (Krauss, 1949; Sanford, 1962).

As noted previously, these morphological and anatomical features result in low evapotranspiration (ET) (Ekern, 1965) and extreme tolerance to drought. Transpiration values of 1.3 mm day^{-1} on cloudy days and 2.7 mm day^{-1} on fine days, average 2.1 mm day^{-1}, were obtained for 15–16-month-old fruiting pineapple plants (Shiroma, 1973). In a pot study in sandy soil, transpiration was maximum during the summer when temperature and solar radiation were highest (respectively about 27°C and 10–12 MJ m^{-2} day^{-1}) (Shiroma, 1971); a low value of 0.4 mm day^{-1} was estimated during the coldest periods. Average ET values for 'Smooth Cayenne' pineapple in field experiments in Hawaii were 0.83 mm day^{-1} with a plant-trash mulch and 1.25 mm day^{-1} with plastic mulch (Ekern, 1965). For a leaf canopy formed by small plants (LAI = 4.2) during fruit development, daily maximum ET was 1.3 mm on cloudy days (irradiance = 10.7 MJ m^{-2}) and 2.7 mm on a sunny day (irradiance = 16.6 MJ m^{-2}), with an average of 2.1 mm day^{-1} (Shiroma, 1973). Measurements of ET made in Côte d'Ivoire (N'Guessan, 1985) showed that values decreased from 0.25 mm h^{-1} over a 10 h period 5–6 months after planting to 0.11 mm h^{-1} per 10 h period 7–10 months after planting. However, ET in Côte d'Ivoire can reach 4.5 mm day^{-1} when solar radiation is high (Combres and Perrier, 1976). With irrigation, ET averaged 3.0 mm day^{-1} over a 2-month period (Combres, 1979).

Drought

Despite the high resistance of pineapple to drought, effects of drought on plant morphology and growth are important. In a dry season, the width of young leaves, the rate of leaf emergence and the weight of successive 'D' leaves may be reduced (Py, 1965). In Hawaii, leaf elongation decreased when the soil moisture content declined below 30–35% (Ekern, 1964). During the dry season in Côte d'Ivoire, water content was less and specific leaf area (SLA) (g m^{-2}, fresh weight basis) was greater in unirrigated than in irrigated crops (E. Malézieux, unpublished results). The symptoms of drought develop slowly, the earliest being reduced growth and wilting of the older leaves (Swete Kelly and Bartholomew, 1993). With severe and prolonged drought, leaf colour changes from dark to pale green, then to pale yellow and finally to red. At the later stages, leaf margins curl downward, leaves lose their turgidity and become limp and growth stops (Py *et al.*, 1987; Swete Kelly and Bartholomew, 1993).

The effects of drought are reversible and, when water again becomes available, the leaves rehydrate and normal growth resumes. Leaves not yet fully expanded resume their growth. Leaf width rapidly increases, resulting in a constriction at the point where elongation resumed (Py *et al.*, 1987). Such leaves generally develop spines on the margins at the point where growth was restricted. Symptoms of water stress may appear more rapidly where soil water-holding capacity is low, if rooting depth is restricted or if the root system has been damaged by pests or disease (Swete Kelly and Bartholomew, 1993).

Temperature

Leaf and plant temperatures of this relatively non-transpiring crop reach values that are detrimental, perhaps even lethal, to mesophytic crops. The temperature of horizontal leaves of 6-month-old 'Smooth Cayenne' plants reached 48°C between 1 and 3 p.m. in Hawaii (Aubert and Bartholomew, 1973). The difference between the leaf middle and base reached 18°C and the maximum difference between leaf and air temperatures was 18.6°C at 1 p.m. Such extreme leaf temperatures caused no permanent harm, but their specific effects on physiological processes have not been studied. As discussed previously, the effects of temperature on stomatal conductance are significant.

The effect of temperature on growth is quite complicated. The morphology of 'Smooth Cayenne' plants is markedly

affected by temperature. Optimum nutrition in environments having a controlled night temperature greater than about 25°C and in warm, humid, low-altitude climates near the equator produces plants with numerous, wide, flaccid leaves (Fig. 5.8; Py *et al.*, 1987; Bartholomew and Malézieux, 1994). Conversely, in controlled environments with cool night temperatures (Friend, 1981) and in cooler climates, leaves are erect, straight, rigid, shorter and fewer in number (Fig. 5.8; Py *et al.*, 1987; Bartholomew and Malézieux, 1994). In Hawaii, leaves of plants grown in high, cool elevations are shorter and more rigid than those on plants grown at lower elevations.

Indices such as SLA (leaf area per unit of leaf dry mass, $m^2\ kg^{-1}$) and leaf area ratio (LAR) (leaf area per unit of total plant dry mass, $m^2\ kg^{-1}$) allow the effects of temperature on plant morphology to be quantified and extend our ability to predict the effects of environment on vegetative growth. Whole-vegetative-plant SLAs over time were consistently lower for plants grown at night temperatures of 18, 22 and 26°C than for those grown at 30°C (Fig. 5.9). The lowest SLA was about 3.8 $m^2\ kg^{-1}$ dry weight at a day/night temperature of 22/18°C (Bartholomew, 1982). SLA declines gradually as plant mass and age increase (Fig. 5.9), especially at the cooler night temperatures, so comparisons of SLA between plants in different environments must be made using plants having approximately the same mass.

Growth slows when night temperatures are cool, and a lower SLA at such temperatures will further reduce the rate of increase in LAI and prolong the time required to reach full canopy closure and complete interception of available light. Thus, the rate of leaf area expansion will probably decrease more rapidly as night temperature decreases than would be predicted just on the basis of the effects of temperature on leaf elongation. Mitigating this effect of cool temperature, at

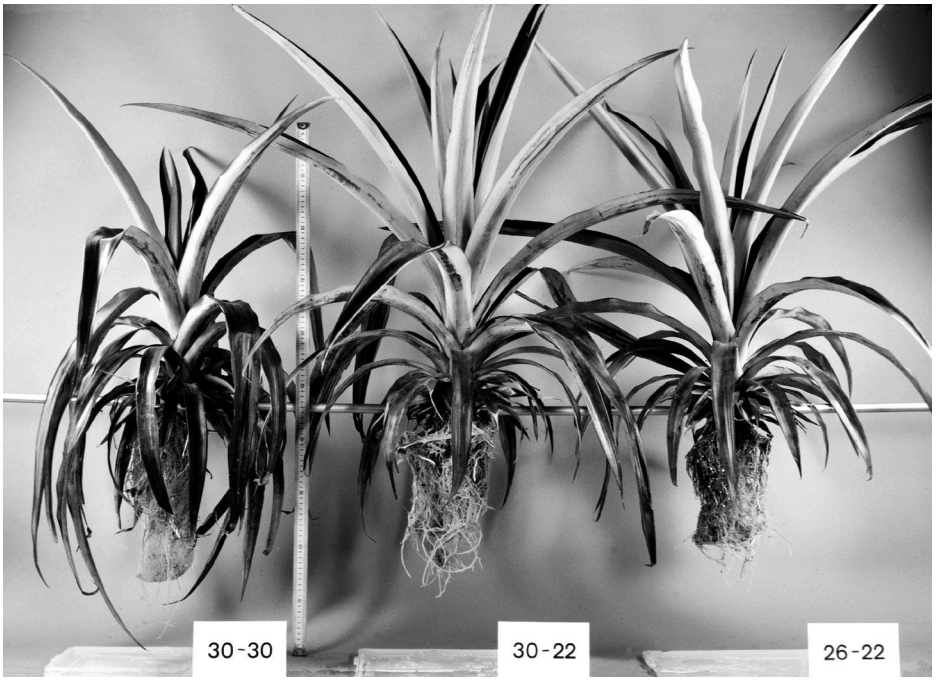

Fig. 5.8. Effects of warm (30°C) and cool (22°C) night temperatures on the leaf orientation of 'Smooth Cayenne' pineapple. The plants were grown for 5 months at the indicated temperatures. (Photo of D. Bartholomew.)

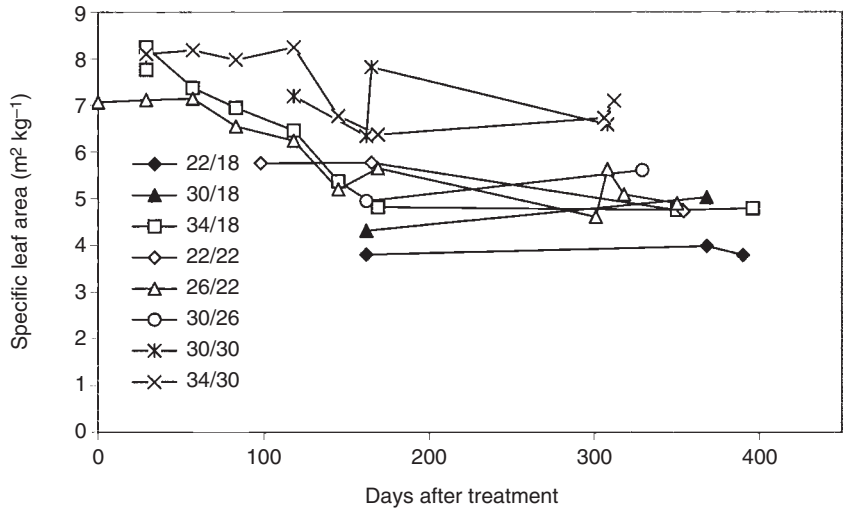

Fig. 5.9. Effects of day and night temperature (°C) on the specific leaf area (SLA) (m^2 kg^{-1} dry weight) of the green leaf tissue of 'Smooth Cayenne' pineapple grown in controlled environments. Pineapple crowns were started in a 26/22°C day/night temperature environment and transferred to the various temperatures 100 days after planting. Notice the gradual decrease in SLA with increasing time after planting. At a given harvest date, larger plants generally had a lower SLA than did smaller plants. Plants harvested after 400 or more days had produced fruit at night temperatures of 18 and 22°C while plants at warmer night temperatures remained vegetative. Data points are means of total green leaf area (white and pale green basal tissue removed) and dry weight for two plants. (Redrawn from Bartholomew and Malézieux, 1994.)

least to some degree, is the fact that plants growing in cooler environments have a higher net assimilation rate, which would offset to some degree the benefit imparted by a more rapid rate of leaf expansion that would occur in warm environments. Thus, dry-matter gain by plants in cooler environments may be as high as that which occurs in warmer environments, where leaves expand more rapidly. Unfortunately, simultaneous changes in other climatic factors as temperature changes, possible differences in the growth rate of 'Smooth Cayenne' clones and differences in quality of management make it very difficult to compare productivity across environments having different temperature regimes.

Consistent with the effect of temperature on SLA, LAR values for the 'Smooth Cayenne' clone 'Champaka F-153' also generally increased with increasing night temperature (Fig. 5.10) and decreased with increasing plant age. An increase in LAR was also observed for plants grown in the field as elevation decreased and average temperature increased (Fleisch, 1988). The SLA and LAR, both on a dry-mass basis, were related to average air temperature (T) by the equations:

$$\text{SLA} = 1.93T + 3.5,\ R^2 = 0.33 \quad (4)$$
$$\text{LAR} = 1.07T + 64.6,\ R^2 = 0.37 \quad (5)$$

where SLA is expressed in cm^2 g^{-1} and T in °C. The relatively low R^2 values for equations (4) and (5) are assumed to be due, at least in part, to the decrease in SLA and LAR with increasing plant mass and age.

In contrast to many crops (Biscoe and Gallagher, 1977) and regardless of the air temperature, the leaves of the pineapple mother plant persist at least into the first ratoon in Hawaii, a period of more than 24 months. However, the functionality of pineapple leaves of various ages has not been adequately determined.

Both the 'Smooth Cayenne' pineapple leaf and stem are important storage organs and can accumulate large quantities of starch.

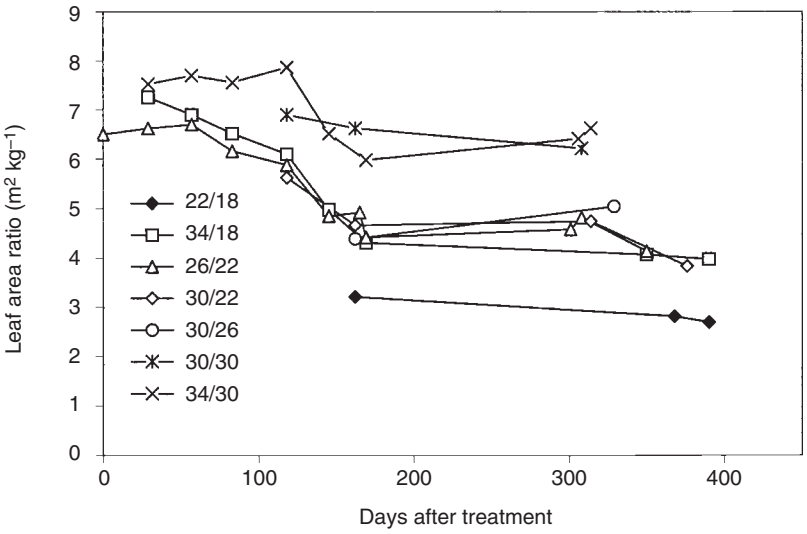

Fig. 5.10. Effects of day and night temperature (°C) on the leaf area ratio (m^2 of leaf kg^{-1} dry weight of plant) of 'Smooth Cayenne' pineapple grown in controlled environments. Pineapple crowns were started in a 26/22°C day/night temperature environment and transferred to the various temperatures 100 days after planting. Data are means for two plants. (Redrawn from Bartholomew and Malézieux, 1994.)

The stem of a crown at the time of fruit maturation can contain more than 20% starch on a dry basis. Stem fresh weight increases slowly during the first months after planting and during this time, starch and dry matter content initially decline and remain at about 10–12% for several to many months – about 9–11 months in Hawaii (Pineapple Research Institute of Hawaii, personal communication). In Hawaii, dry-matter content and stem starch then begin to increase and stem dry-matter content can reach 30% (Fig. 5.11) and starch can exceed 60%, dry basis, at the time of flower induction (Bartholomew and Paull, 1986). At a plant population density of 4.3 plants m^{-2}, at 458 days after planting when flowering was forced, stem starch accumulation reached about 325 g m^{-2} of ground area (Pineapple Research Institute of Hawaii, personal communication). About 90 days later, starch mass per unit of ground area exceeded 800 g m^{-2}. In environments warmer than Hawaii, there may be no increase in stem dry-matter content until vegetative growth is interrupted by forced induction. Data for controlled conditions showed that, at night temperatures of 26 or 30°C, plants had lower dry-matter content and little starch in the stem, while plants grown at night temperatures of 18 and 22°C had significant amounts of starch (Bartholomew and Paull, 1986). Plant dry-matter and starch content are believed to be especially important after floral induction (see Bartholomew *et al.*, Chapter 8, this volume).

While stem starch levels at the time of floral induction can be as high as 60% in Hawaii, starch levels do not reach 20% at the time of forcing in Côte d'Ivoire, where temperatures are higher. Forcing occurs much sooner after planting in Côte d'Ivoire than in Hawaii, because suckers are the primary source of planting material and vegetative growth is more rapid in the warm environment. Because the LAR increases as night or average temperature or both increase, large differences exist between statistical models of vegetative growth developed in Hawaii (Fleisch, 1988; Zhang, 1992) and in Côte d'Ivoire (Malézieux, 1991).

Leaf dry-matter content also gradually increases with time during vegetative and early reproductive growth (Fig. 5.11) and,

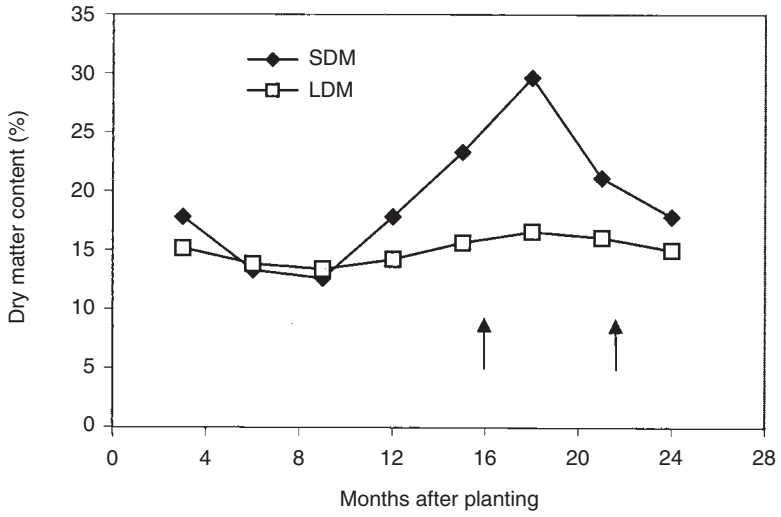

Fig. 5.11. Dry-matter content of 'Smooth Cayenne' pineapple stem (SDM) and leaves (LDM) from 3 months after planting in December 1932 until after plant-crop fruit harvest in July 1934. The arrows indicate the approximate time of natural induction of flowering and of fruit harvest. (Redrawn from King, 1935.)

though such changes are relatively small, when total storage per unit of land area is computed, the accumulation is significant. In an unpublished study conducted in Hawaii (Pineapple Research Institute of Hawaii, personal communication), the starch content of leaves sampled early in the morning averaged about 0.25% for the first 400 days after planting. Starch then gradually increased to 1.27% at 570 days after planting (120 days after forcing). At that time, plants had accumulated an average of 254 g m^{-2}, land-area basis, of starch in leaves. Both stem and leaf starch declined sharply after floral induction, presumably as reserves were drawn upon to support fruit and sucker growth. In tropical environments, little starch is accumulated in plant tissues by the time of forcing, so growth of fruit and propagules such as suckers, is dependent on current photosynthesis. In these environments, propagule development is delayed until after the fruit is harvested.

Changes in plant dry-matter content and partitioning with changing root temperature at ambient air temperature were similar to the effects of temperature observed in controlled environments. Leaf dry-matter content decreased from 16.5 to 12% as the root temperature increased from 15 to 30°C (Ravoof, 1973). Also, as root temperature increased, the percentage of dry matter allocated to leaves increased from 77 to 80%, while that allocated to stem decreased from 17 to 13% (Ravoof, 1973). Plant LAR probably increased as root temperature increased.

Light interception

The spectral properties of the adaxial surface of pineapple leaves over the wavelength range from 520 to 750 nm were not significantly different from those of wheat, olive, orange and peach (N'Guessan, 1985). However, pineapple leaves have very low reflectances in the infrared region with minima at 1440 and 1990 nm (water peaks). Despite reflectances in the visible range comparable to those of mesophytes, much of the radiant energy falling on a pineapple plant is entrapped by multiple reflections within the rosette leaf array (Ekern, 1965). As a consequence, the total reflectance of the canopy is low (Ekern, 1965), resulting in canopy albedos that ranged from 0.14 to 0.16 for canopies ranging in age from 1 to 16 months (Shiroma, 1973; Combres, 1983). There was no significant variation in albedo with canopy height (N'Guessan, 1986).

Estimated canopy light extinction coefficients for pineapple are typical of canopies with a relatively erect leaf orientation. Extinction coefficients (k) of 0.56–0.59 were calculated for 'Smooth Cayenne' pineapple in Hawaii (Fleisch, 1988; Zhang, 1992), resulting in 95% light interception at an LAI of about 5.0. Extinction coefficients for mesophytic crops typically range from 0.4 for erectophile canopies to 0.8 or greater for planophile ones (Russell *et al.*, 1989). A significantly lower k of 0.29 was found for pineapple in Côte d'Ivoire by measuring total radiation interception of pineapple crops with a somewhat wider row spacing (Malézieux, 1991). Low k values account in part for the ability of pineapple to sustain very high LAIs.

Photoperiod and irradiance

The data on the effects of photoperiod and irradiance are sparse and few useful generalizations can be made from them. Also, changes in these parameters in natural environments are often confounded with temperature. At low light, seedling leaf lengths decreased as the PPF increased from 100 to 325 μmol m^{-2} s^{-1} (Aromose, 1989). Average leaf length was greater in 16 than in 8 or 24 h photoperiods (Aromose, 1989). At an average PPF of 400 μmol m^{-2} s^{-1}, the length of the longest leaf of plants grown for 692 days in controlled conditions increased as photoperiod increased from 6 to 10 h, was unchanged at 12 h and declined sharply at 16 h (Friend and Lydon, 1979). The width of the longest leaf increased continuously with increasing photoperiod while leaf thickness (g cm^{-2}, fresh weight basis) declined (Friend and Lydon, 1979).

In natural environments, leaves of plants grown in low irradiance are long, erect and dark green, while those of plants grown in very high irradiance become red or even yellow (Py *et al.*, 1987). Physical damage and death, typically referred to as sunburn, due to high irradiance was reported in India (Srivastava and Singh, 1971). Connelly (1969) found that average 'D'-leaf length was 52 cm in full sun, 55 cm in 25% shade and 50 cm in 50% shade.

Effects of environment on vegetative growth

Specific effects

TEMPERATURE. The plant growth rate of pineapple is strongly influenced by temperature but few studies have been made in controlled environments and the results from field studies can be difficult to interpret. Leaf and root elongation rates measured in controlled environments over a range of temperatures (Sanford, 1962) generally show good correspondence with the results of later studies. The optimum temperature for leaf growth was 29°C and that for roots was 32°C (Sanford, 1962). Growth of both organs was greatly reduced at temperatures below 20°C and ceased at about 10°C.

Data on the long-term effects of temperature on dry-matter accumulation are sparse and such data are needed if the vegetative growth responses in the diverse field environments where pineapple is grown are to be interpreted. Pineapple plants grown in controlled environments having night temperatures of 26°C or less had greater weights than those grown in environments having 30°C night temperatures, and the differences increased over time (Fig. 5.12; Bartholomew, 1982). After about 400 days, plants grown at cooler night temperatures accumulated two to three times the dry mass of those grown at 30°C night temperatures (34/30 and 30/30°C). In environments with warm days (26–34°C) and cool nights (18–22°C), plants also had higher dry-matter contents and greater plant relative growth rates and leaf growth rates than did plants grown in warm days and warm (30°C) nights (Bartholomew, 1982). Plant leaf area at the end of the study was also greatest for plants grown at 30°C day and 26 or 22°C night temperatures (Fig. 5.13). The more rapid growth of plants at the cooler night temperatures resulted mainly from higher net assimilation rates. Net assimilation rates on a unit leaf basis ranged from about 1.0 g m^{-2} day^{-1} for plants grown at 30°C dark temperatures to 2.0 g m^{-2} day^{-1} for plants grown at dark temperatures of 26 or 22°C (Bartholomew, 1982). Friend (1981) also reported that plants grown at a 30°C night temperature were smaller than those grown at cooler night temperatures.

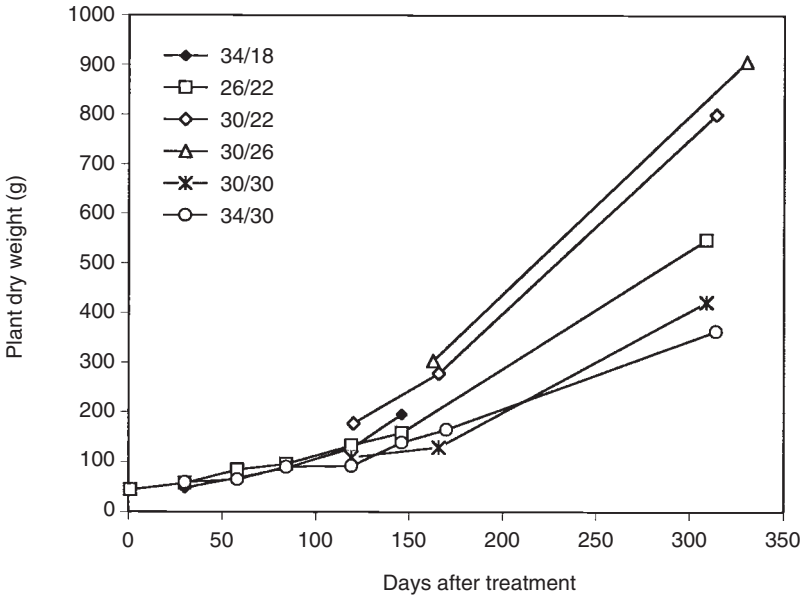

Fig. 5.12. Effects of day and night temperature (°C) on growth in dry mass of 'Smooth Cayenne' pineapple plants grown in controlled environments. Pineapple crowns were started in a 26/22°C day/night temperature environment and transferred to the various temperatures 100 days after planting (day 0 in the figure). Each data point is the mean for two plants. (Redrawn from Bartholomew and Malézieux, 1994.)

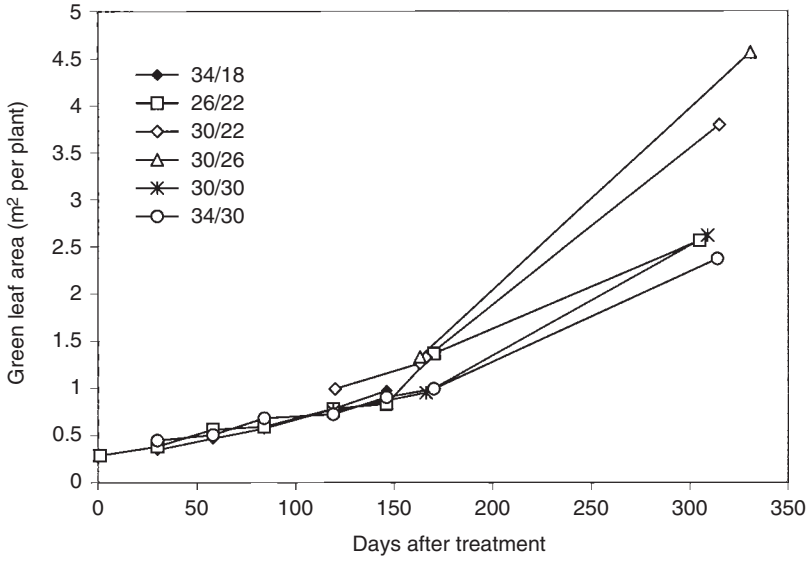

Fig. 5.13. Effects of day and night temperatures (°C) on growth in green leaf (white and pale green leaf basal tissue excluded) area per plant of 'Smooth Cayenne' pineapple plants grown in controlled environments. Pineapple crowns were started in a 26/22°C day/night temperature environment and transferred to the various temperatures 100 days after planting (day 0 in the figure). Each data point is the mean for two plants. (Redrawn from Bartholomew and Malézieux, 1994.)

Under field conditions, the mother plant relative growth rate for the period from about 2 months after planting to induction of flowering was reduced by the cool winter temperatures of south Queensland (Sinclair, 1992). When data from Hawaii and Côte d'Ivoire are compared, plants grown from crowns in Hawaii have 0.7 m^2 of leaf area 8 months after planting and would be grown another 4–6 months before forcing (Bartholomew and Kadzimin, 1977). In Côte d'Ivoire, plants of the same age grown from larger suckers would have 1.8 m^2 of leaf area and would be ready to be forced (Malézieux, 1991). Some of the difference in size of plants after 8 months of growth is almost certainly due to the larger propagules used in Côte d'Ivoire, but some of the difference is also probably due to the more rapid expansion of leaf area in the tropical environment of Côte d'Ivoire. In Thailand, large suckers, some weighing up to 2.0 kg, are planted and these will be forced within 5–6 months after planting.

It seems appropriate to interject here that, while much has been written about the relative advantage of suckers over smaller propagules (shorter time from planting to forcing; larger average size of fruit), only fairly recently has it been recognized that the size of the propagule is the main factor accounting for the difference. A large propagule produces a large plant more quickly than does a small propagule.

In areas where there is considerable seasonal variation in climate, time of planting can also affect time from planting to forcing. In Hawaii, crowns will be forced 12–14 months after planting (A. Hepton, personal communication). Propagules planted during periods of cool weather and low irradiance establish and grow more slowly than do those planted when weather conditions are more favourable for growth.

Theoretically, growth in leaf area depends on the rate of both leaf initiation and expansion. Leaf expansion, as indicated by rate of elongation, increased with temperature up to 29°C (Sanford, 1962). Leaf expansion was also greater where the day/night temperature differential was large than where it was small and night temperature was high (Bartholomew, 1982). A relatively sharp temperature optimum occurs for leaf elongation rate (Sanford, 1962), but no such sharp optimum was observed for dry-weight gain, presumably because of morphological and anatomical differences induced by temperature or the day/night temperature differential, or both.

Leaf initiation in natural environments, as indicated from rates of leaf appearance, is sensitive to temperature. In Taiwan, the equation:

$$NLEAF = 18.125 \times \log_{10} T/11.669 \qquad (6)$$

where T is mean monthly temperature in °C and $NLEAF$ is number of leaves to appear in 1 month, indicates the extent to which leaf appearance rate is influenced by temperature (Shiroma, 1972). Data on leaf emergence collected from fields at elevations of 91, 305 and 792 m in Hawaii could be described by a similar relationship (D.P. Bartholomew, 1988, unpublished results). In Côte d'Ivoire, which has a high mean air temperature and narrow diurnal variation, the number of leaves appearing per 2 months was best described by a quadratic function and showed an optimum temperature at about 26–27°C (E. Malézieux, 1992, unpublished results). Similar results showing the existence of an optimum temperature near 28°C were obtained in Hawaii (J. Zhang, 1992, personal communication).

Leaf number can be predicted using heat accumulation or daily thermal time (DTT) (Zhang *et al.*, 1997). An enhanced model was developed which also accounted for the reduction in growth that occurs at low (below 16°C) and high temperatures (greater than 35°C). Such temperatures would normally be reached only during part of the day (Zhang *et al.*, 1997). DTT was calculated for each day by the equation:

$$DTT = TM - BT \qquad (7)$$

where TM is the mean temperature and BT the base temperature. A BT of 16°C provided the best fit for the data. For a minimum temperature $<$ BT or a maximum day temperature $>$ 35°C, DTT was calculated using a procedure similar to that reported by Malézieux *et al.* (1994) for the estimation of

daily fruit thermal time. The leaf-emergence model was calibrated and validated with data from Hawaii and Côte d'Ivoire. Based on Celsius temperature, the phyllochron (interval between the appearance of two successive leaves) was 50 degree-days per leaf. Interplant competition had a significant effect on leaf number, and it was assumed that this effect was due to a reduction in meristem temperature caused by the intense shading that occurs at high plant population densities. This effect was simulated in the model using interplant competition factors calculated from leaves m^{-2} of ground area (Zhang *et al.*, 1997).

In addition to the effects of root temperature on dry-matter partitioning noted above, Ravoof (1973) also showed that the total fresh mass of 40-day-old plants grown from slips increased with increasing root temperature from 15 to 30°C, though the increase in growth was not proportional to the increase in root temperature. In Okinawa, Japan, a relatively cold climate for pineapple (mean temperature ≈ 17°C, minimum temperature for more than 1 month ⩽ 6°C) and in Hawaii during the winter (mean temperature ≈ 22.3°C), growth is enhanced by black polyethylene-film mulch (Ekern, 1967; Ogura *et al.*, 1968). The 33% increase in growth in Hawaii resulted from a soil temperature increase of only 1.6°C. In the Canary Islands, where mean average air temperature is about 20°C, both black polyethylene mulch and a polyethylene cover over the plants increased yields (Galan Sauco *et al.*, 1988b).

IRRADIANCE AND PLANT POPULATION DENSITY. Few studies have been conducted on the effects of irradiance on vegetative growth. Connelly (1969) found that estimated plant weight of 'Smooth Cayenne' plants grown in pots was unaffected by 25% shade but was reduced by 20% under 50% shade. Less nitrogen was required for optimum growth at low than at high light.

In most crops average plant mass decreases with increasing plant population density due to interplant competition for light, but no data illustrating this effect on pineapple were found (Bartholomew and Kadzimin, 1977; Py *et al.*, 1987; Scott, 1992). This surprising result is assumed to be due to the fact that researchers who studied the effects of plant population density on pineapple generally did not collect data on plant fresh or dry mass, did not report such data or estimated plant mass from 'D'-leaf mass. 'D'-leaf mass is a faulty estimator of plant mass, because as plants get larger, 'D'-leaf mass reaches a maximum, while leaf number and leaf and plant mass continue to increase (Py *et al.*, 1987).

Interplant competition does occur during vegetative growth of pineapple, and growth is reduced at high plant population densities (Malézieux, 1992a; Zhang, 1992). In a study in Hawaii, there was no reduction in plant mass with increasing plant population density for the first 200 days after planting, even at a density of 123,500 plants ha^{-1}, and light interception did not reach 95% at that density until about 350 days after planting (Zhang, 1992). Plant mass at forcing, which occurred for plantings made in June, August and October at approximately 440, 380 and 335 days, respectively, after planting, decreased significantly with increasing density at all planting dates. Similar results were obtained in Côte d'Ivoire (Malézieux, 1992a). In the latter experiment, plant mass 8 months after planting increased by 33 and 20%, in irrigated and unirrigated conditions, respectively, as plant population density decreased from 100,000 to 20,000 plants ha^{-1}. It is clear that competition for light occurs during vegetative growth in pineapple fields even at moderate planting densities. However, it may not be detectable where growth is limited by water or other stresses. Unless the relationship between 'D'-leaf weight and plant mass is known, 'D'-leaf weights should not be used as an indicator of plant mass beyond about 6 months after planting, or earlier than that where large suckers are planted. The effects of plant population density on fruiting are discussed in detail later (see Bartholomew *et al.*, Chapter 8, this volume).

Lest the details obscure the important message, it is clear that total biomass and often total yield increase with increasing plant population density. However, studies often show that, at densities much above

74,000 plants ha^{-1} and sometimes well below that, the percentage of fruit recovered, as well as the quantity and quality of products, declines.

Allometric data help to explain the effects of plant population density on vegetative growth. Leaf appearance rate decreased with increasing planting density (Norman, 1977; Malézieux, 1992; Zhang, 1992) and, in one study, leaves were longer and narrower at the higher planting densities (Wee, 1969). Specific leaf mass (SLM) (dry-mass basis) was significantly decreased when planting density was higher than 6 plants m^{-2}. However, at the base of the leaf, fresh weight per unit area increased at high densities (Malézieux, 1992a). Zhang (1992) reported that SLA at 300 days after planting was related to planting density (PD) by the equation:

$$SLA = 50.3 + 0.51PD \quad (8)$$

and the effect was highly significant.

The production of vegetative propagules, such as slips and suckers, requires an input of carbohydrates, at least until they develop sufficient leaf area to become autotrophic. Competition for light at higher planting densities is assumed to reduce the supply of assimilates available for growth and for storage reserves, because the number of slips and suckers per plant decreases at higher plant populations (Lacoeuilhe, 1974; Py *et al.*, 1987). For clones that produce slips, slip numbers decrease at a faster rate with increasing plant population density than do suckers (Py *et al.*, 1987). Suckers per unit area may increase or, as occurred in a recent study, become normalized across planting density (Scott, 1992). Scott (1992) showed that, as plants per hectare increased from 46,112 to 80,650, suckers per plant decreased from 1.84 to 1.11. Thus, despite a wide range of planting densities, suckers ha^{-1} only ranged from 82,162 to 89,572 (Scott, 1992).

In addition to reducing the number of suckers per plant, sucker development, which in Australia (Sinclair, 1992) and Hawaii is initiated at the time apical dominance is broken by forcing fruit development, may also be delayed at higher planting densities. Circumstantial evidence suggests that, when interplant competition is intense, there is insufficient photosynthate for the development of both a fruit and suckers. The fruit is a stronger sink than developing suckers, since forced plants will always develop a fruit but may not develop suckers until after the fruit matures. In tropical regions, such as Côte d'Ivoire, sucker growth was increased up to 20% by cutting off the leaves that extend above the developing suckers immediately after fruit harvest (Combres, 1983). Leaf removal may improve sucker exposure, thus promoting their growth.

DROUGHT. Despite the xeromorphic characteristics of pineapple, growth and yield are significantly reduced when drought is prolonged. One effect of a water deficit is to reduce the number and length of the roots (Kadzimin, 1975; E. Malézieux and G. Godo, 1991, unpublished results). White root tips visible in the soil, expressed as a percentage, have been used as an indicator of root health and water deficit (Sanford, 1962; Fig. 5.14), and root elongation ceases and root tips suberize when the soil moisture approaches –1.5 MPa (Ekern, 1967). Suberization does not protect roots indefinitely as they will die if the soil moisture stress is severe and prolonged (Krauss, 1959). In Côte d'Ivoire, rooting depth and root numbers increase with irrigation or with polyethylene mulch (E. Malézieux and F. Zampatti, 1991, unpublished results).

Most of the quantitative data on the effects of water stress on growth were obtained on plants grown in pots; few data were found on the effect of water deficit on vegetative growth rate. Sideris and Krauss (1928) found that plants did not grow in soils containing 5% moisture and, relative to well-watered soil, growth decreased significantly in soils containing 10 or 15% moisture. Growth was not different in soils maintained at 20, 25 and 30% moisture. In another pot study, growth in a loamy soil continued at a soil moisture content of 10% but almost stopped when soil moisture fell to 5% or less (Shiroma, 1971). In a pot study where the irrigation interval was varied from twice weekly to bimonthly, 'D'-leaf weight, leaf area, dry weight of all plant parts and fresh

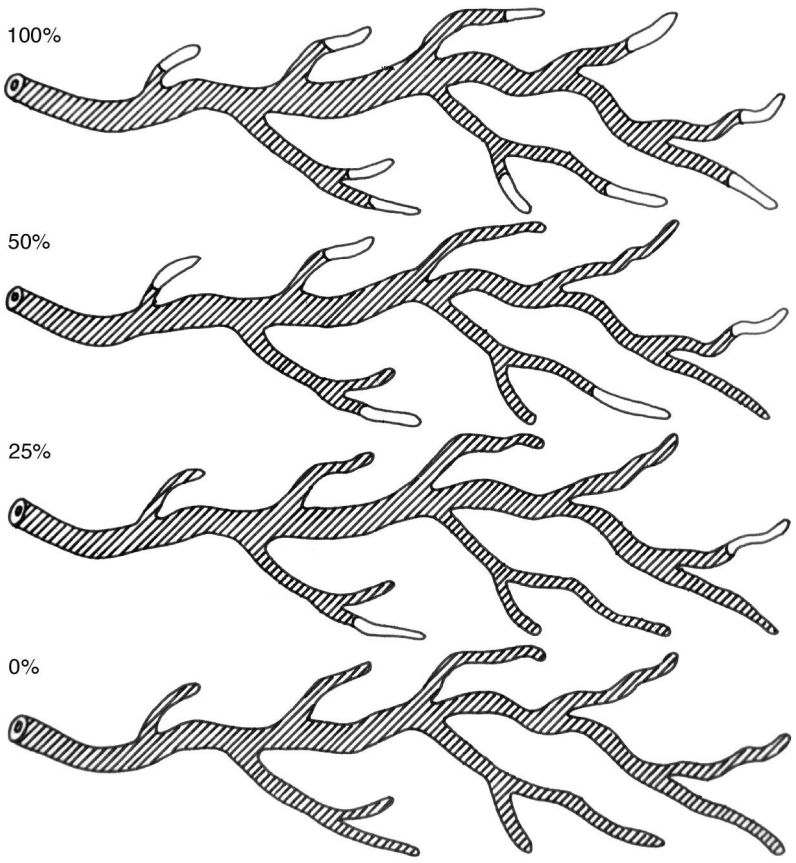

Fig. 5.14. Variation in the percentage of white root tips used to diagnose root health and water availability (modified from Nightingale, 1949).

fruit weight all decreased significantly as the irrigation interval was extended (Chapman *et al.*, 1983). After an early establishment period, Kadzimin (1975) grew pineapple in black polyethylene bags for 7 months at average soil water potentials (Ψ_{soil}) of –0.1, –0.5, –1.0 and –1.5 MPa and in an unirrigated treatment. In that study, plant total dry mass decreased 27.6, 32.4 and 46.9%, respectively, in the –1.0 and –1.5 MPa and unirrigated treatments. Only leaf and stem growth were reduced at –1.0 MPa; in the –1.5 MPa and unirrigated treatments, leaf, stem and root growth were reduced. The root system as a proportion of the whole plant decreased significantly in the –1.5 MPa and unirrigated treatments. It was suggested that the decrease was due to a reduction in meristematic activity associated with the internal water deficit (Kadzimin, 1975). In the clay soils of Hawaii, where water-holding capacity is high, irrigation begun when Ψ_{soil} reached –0.4 MPa was equal to or better than irrigating at a Ψ_{soil} of –0.03 or –0.07 MPa (Thorne, 1953). However, where soils are sandy and soil water-holding capacity is low, growth was reduced as soon as the Ψ_{soil} fell below –0.015 MPa at a 15 cm depth (Combres, 1979). Combres (1979) concluded that a Ψ_{soil} of –0.015 could be used as a threshold value to initiate irrigation (Combres, 1983).

Plant moisture content decreases with increasing soil moisture stress and the thick-

ness of the leaf water-storage tissue (Fig. 5.15) decreases as the plant water deficit increases (Fig. 5.16). However, leaf water content changes slowly and pineapple tolerates long periods of drought with minimal plant loss. Nose *et al.* (1981) observed only a 0.1% decrease in leaf water content as soil pF – a measure of soil water status – decreased from 1.1 to 4.5. Chapman *et al.* (1983) reported that the water content of 'D' leaves was not significantly reduced by any irrigation treatment until fruit harvest and, even then, differences in the 'D'-leaf moisture contents for the high and low water treatments were small. Even uprooted plants lose water slowly. Fruiting suckers removed from their mother plants at flowering and kept without water for 3 months on a glasshouse bench in sunlight lost 44.4% of their fresh weight by transpiration, while comparable shaded ones lost 41.6% (Sideris and Krauss, 1955). Despite the high degree of dehydration, significant fruit growth occurred. Water losses from the leaves due to translocation to the fruit were estimated at 18 and 26.8% of leaf weight for the sun and shade plants, respectively. Pineapple plants show a remarkable ability to transfer water and other nutrients from the leaves to the fruits when water stress is extreme.

Though normal values of pineapple leaf water potential (Ψ_L) were about –0.6 MPa at a Ψ_{soil} of –0.1 MPa, Ψ_L reached –2.3 MPa at a Ψ_{soil} of –1.8 MPa (Kadzimin, 1975). George *et al.* (1984) found that Ψ_L of pineapple leaves varied from –0.2 to about –1.8 MPa after 12 weeks without any water supply, while leaf relative water content (RWC) decreased from about 96% to 42% over the same time period. Leaf RWC and Ψ_L were linearly correlated with a 10% change in RWC corresponding to a 0.28 MPa change in Ψ_L (George *et al.*, 1984). Similarly, Kadzimin (1975) found that, as Ψ_L decreased from –0.1 MPa for well-watered plants to –2.2 MPa for unirrigated plants, leaf RWC decreased from 96% to 70%.

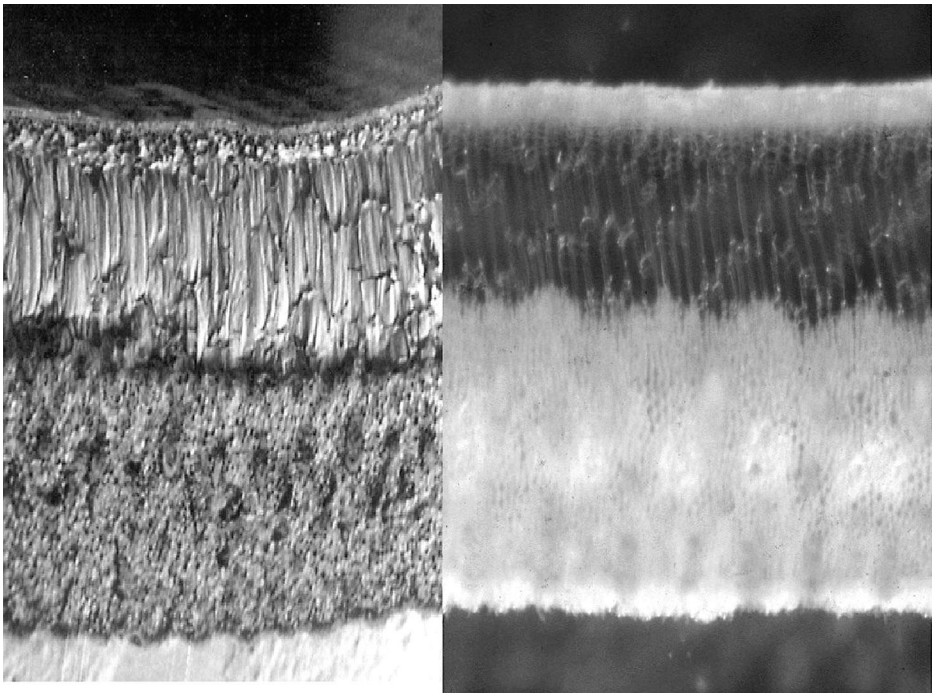

Fig. 5.15. Light and scanning electron microscope cross-sections of a mature pineapple leaf showing the prominent water-storage tissue on the adaxial side of the leaf and the chlorenchyma on the abaxial half of the leaf (photos of D. Bartholomew).

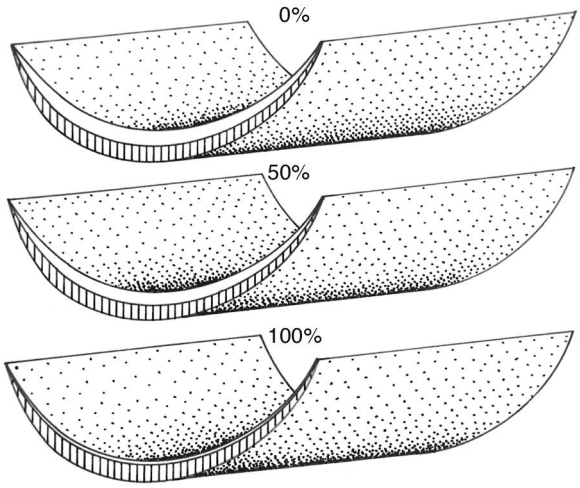

Fig. 5.16. Leaf water-storage tissue deficiency (%) at inflorescence emergence (red bud) with decreasing availability of water (modified from Nightingale, 1949).

However, leaf RWC was concluded to be a rather insensitive indicator of water stress in pineapple, especially under minimal stress situations (Kadzimin, 1975; George *et al.*, 1984).

Pineapple plants subjected to water stress have significantly lower ET values compared with unstressed plants. In central Côte d'Ivoire, ET of complete pineapple leaf canopies averaged 3.8 mm day^{-1} when irrigated and 2.9 mm day^{-1} when unirrigated (Combres and Perrier, 1977). The ET/ET_g ratio, where ET_g is the potential ET of a grass cover, is about 0.45 for an irrigated pineapple crop but the ratio decreases during drought (Combres, 1983).

ET of a pineapple crop depends both on the stage of development and climatic conditions. When well watered, the ET of complete canopies ranged from 0.6 to 0.7 of the potential evaporation of a grass cover (Combres and Perrier, 1977). The crop parameter K_c, in the equation:

$$ETR = K_c \times ET_o \quad (9)$$

where ETR is actual ET and ET_o is standard evaporation (Priestley and Taylor, 1972), generally ranges between 0.8 and 1.3 for most crops. An average value of 0.74 was observed for pineapple (Combres, 1983), but K_c can vary significantly over the plant cycle. K_c decreased significantly from 0.93 5 months after planting (50–60% of soil cover) to 0.41 by 11 months after planting, at which time there was 80–90% of soil cover by the canopy (N'Guessan, 1985). Where pineapple was planted through a polyethylene mulch in Hawaii, a 50% decrease in the daily rate of consumptive use of water occurred by the time of 60% canopy closure (Ekern, 1964). It is a striking feature of pineapple that the ET rate of a pineapple crop decreases as the plant develops and the canopy cover increases, whether in mulched or unmulched conditions (Ekern, 1964). With mulch, 15% of the incident energy was used for ET after the canopy closed. The very low water-use rate of pineapple, which is due to the inverted pattern of stomatal conductance and xeromorphic anatomical features, is further reduced by water stress.

FLOODING. Excess water can reduce the growth and yield of pineapple, mainly when waterlogging occurs during root initiation and at fruit filling. As with most crop plants, root growth and efficiency are restricted by inadequate aeration associated with excess soil moisture. In solution cultures, root growth was increased by aerating the

solution (Iwaoka *et al.*, 1935) or by removing roots from the solution for 2 h day^{-1} (Tisseau, 1971). The formation and persistence of root hairs seem to depend upon an oxygen supply to the roots (Py *et al.*, 1987). Root aerenchyma is also increased by a diminished oxygen supply and a comparable effect is seen with an increase in soil compaction (Rafaillac *et al.*, 1978). Excessive water produces a leaf colour change similar to that seen with water stress, in that leaves first become pale yellow and then red, and leaves are reduced in length and are more erect (Py *et al.*, 1987).

General effects

TEMPERATURE. Although there are few specific data on the effects of temperature on the growth and development of pineapple, temperature appears to be one of the most important environmental factors determining pineapple distribution and productivity in the world. Pineapple survives in hot, dry environments where other crops would be non-productive, but is also cultivated in the cool subtropics, where freezing temperatures may occur (Table 5.1). The lowest annual average temperature where pineapple is grown on a commercial scale appears to be 17.2°C in Port Elizabeth, South Africa (Bartholomew and Kadzimin, 1977). In southern Queensland the mean monthly maximum/minimum temperature ranges from 29/19°C in summer to 20.5/6°C in winter (Wassman, 1990). The plant does not tolerate frost, but temperatures have been reported to drop below 0°C for short periods of time in the pineapple-growing areas of south Queensland, Australia (Swete Kelly and Bartholomew, 1993), South Africa, São Paulo, Brazil (Giacomelli and Py, 1982; Py *et al.*, 1987), and southern Florida. As was noted before, prolonged exposures to temperatures less than 0°C can destroy the canopy and lead to the loss of the crop, as has happened in some areas where freezing temperatures can occur (Giacomelli and Py, 1982; Swete Kelly and Bartholomew, 1993). Overhead irrigation has been used to protect against freezes in Florida (J. Tenbruggencate, 1986, personal communication). In the absence of frost, the plant is quite productive in both cool subtropical and tropical environments, though the crop cycle is prolonged in such environments.

Large areas are planted to pineapple in hot, wet intertropical regions, in low-altitude areas and, more specifically, along coastal plains, where the climate is moister and hotter than in continental areas. In most of the tropics, and especially in hot and wet regions close to the equator, the annual range of monthly temperature is very small, sometimes not more than ± 1°C. Thus, the diurnal temperature cycle is often more important than the seasonal cycle (Monteith, 1977).

Optimum day and night temperatures for vegetative growth of pineapple are near 30 and 20°C, respectively, with an optimum mean temperature of 23–24°C (Neild and Boshell, 1976). Plant growth decreases rapidly at mean temperatures below 15°C or above 32°C (Neild and Boshell, 1976). In Hawaii, the slower vegetative growth rates observed from December to April are mainly due to a decrease in the average temperature, especially soil temperature (Ekern, 1967). In Australia, low temperatures from May to October reduce or even stop plant growth in the midwinter period (Glennie, 1981; Wassman, 1986).

The large environmental variation among areas where the crop is grown (Table 5.1) accounts for much of the large variation in the time from planting to maturation of the mother plant crop. Within a given environment, fruit weight at harvest is determined in large part by plant weight at forcing (Py and Lossois, 1962; Gaillard, 1969; Tan and Wee, 1973; Malézieux, 1988; Malézieux and Sébillotte, 1990a). Consequently, an important objective of growers is to obtain a given plant weight at the time plants are to be forced. In the absence of other stresses, plant growth is determined by temperature. For that reason, the interval from planting to forcing varies considerably over the wide range of latitudes and altitudes where pineapple is grown (Table 5.1). In the East London area (33°S, South Africa), where average temperature is 18.8°C (mean minimum temperature of 14.7°C, mean maximum temperature of 22.8°C), the average

period from planting to forcing is 24 months (Bouffin, 1991), whereas in areas near the equator, such as in West Africa, the vegetative growth period is only 6–8 months.

The planting-to-forcing interval also varies with date of planting, especially in areas where the seasonal temperature variation is large. In the Canary Islands, the vegetative cycle ranges from 9 months when planting is done in the spring and plants develop in summer, to 14 months when the crop is planted in winter (Galan Sauco *et al.*, 1988b); similar large variations are encountered in Australia and South Africa. A plant fresh mass of 2.5 kg – a common plant weight for forcing – can be reached within 8 months after planting in Côte d'Ivoire (5°N, mean temperature of 26.6°C), within 10–11 months in Hawaii (21°N, mean temperature of 23°C) and within 13–14 months in Queensland, Australia (26°S, mean temperature of 19°C). As a result, the time from planting to harvest ranges from 12 months near the equator (Gaillard, 1969), where the average annual temperature is 26–27°C, to 32 months in Swaziland (26° 30'S), where mean annual temperature is 16–17°C (Dodson, 1968). While there is wide variability in the length of the vegetative growth phase for 'Smooth Cayenne' in the pineapple-growing areas of the world, there is also considerable variation in the length of the reproductive phase (Table 5.1; see Bartholomew *et al.*, Chapter 8, this volume).

In some pineapple-growing regions, it is common to produce one or two ratoon crops from suckers borne on the mother plant. In equatorial climates, sucker development is commonly delayed until after the fruit matures. The first ratoon crop takes about 1 year in both Hawaii and Thailand, even though growth is more rapid in the warm, humid climate of Thailand. The long period of time required for ratoon-crop development in Thailand results from the fact that suckers do not begin to develop until after the plant-crop fruit is harvested, whereas, in Hawaii, development begins at the time of forcing. In general, the plant and one ratoon crop are harvested after about 2 years in Thailand, 3 years in Hawaii, 3–4 years in Australia (Vuillaume, 1986) and as many as 5 years in Swaziland (Dodson, 1968).

TEMPERATURE INJURY. High temperatures are generally of minor concern during vegetative growth of pineapple. Although leaf and plant temperature may reach very high values due to the low transpiration rate and poor air circulation around the leaves within the plant canopy, leaves tolerate high temperatures well. Leaf sunburn is sometimes seen, but it is not a serious problem in any region where pineapple is grown.

As noted above, low-temperature injury is of greater concern where freezing temperatures are encountered. With mild radiation frost, the upper surface of horizontal leaves develops a red/white-flecked, scorched appearance. If the injury is severe, the whole leaf dies and the leaves become papery. Depending upon the age of the plant when frost injury occurs, vegetative plants may recover and produce an acceptable crop (Swete Kelly and Bartholomew, 1993). Without some sort of frost protection, prolonged exposure to temperatures less than 0°C can destroy the aerial parts of the plant, leading to loss of the crop. As noted above, sprinkler irrigation has been used to protect pineapple plants from freezing in Florida (J. Tenbruggencate, 1986, personal communication).

IRRADIANCE. The significance of irradiance as a factor affecting pineapple yield was recognized at least by the mid-1930s in Hawaii (Sideris *et al.*, 1936). However, there is little evidence that irradiance limits pineapple production in most areas where the crop is grown. Sanford (1962) attributed to Sideris an observation that yield decreases about 10% for each 20% decrease in solar radiation. Shiroma (1977) concluded that irradiance could be limiting for 'Smooth Cayenne' pineapple in Okinawa, but his conclusion was based on lower average global radiation values for Okinawa than for Taichung, Taiwan and Hawaii, rather than data obtained *in situ*. A linear relationship between plant weight 8 months after planting and radiation intercepted by the canopy was established in an experiment in Côte d'Ivoire, where plants were planted every month for 6 years (E. Malézieux, 1992, unpublished results). In this experiment, an

empirical relationship that associated average irradiance during the entire crop cycle and an indicator of drought from planting to harvest explained 64% of the variation in plant weight at harvest (72 monthly plantings with similar cultural practices). However, interpretation of the results of such studies is very difficult because of the long-term nature of the crop and the fact that changes in irradiance are confounded with simultaneous changes in air temperature. In areas where the variation in temperature is small compared with variation in irradiance, such as near the equator, irradiance may be of importance in determining plant growth.

Where both irradiance and temperature change significantly with season, it is very difficult to evaluate the effects of irradiance on pineapple growth and productivity. The quality and average size of the available planting material can vary with time of year (Louis and Nightingale, 1937; Zhang, 1992) and these factors are important because they determine the initial plant size. At a given planting density in the same environment, plant mass at a given time after planting is determined by the mass of the propagule (Py *et al.*, 1987). Even modest differences in propagule mass between plantings in different seasons can obscure the effects of seasonal changes. After a 2–3 month establishment period, which can be further prolonged by cool temperatures or lack of rain, vegetative growth is the product of accumulated irradiance over a period of 6–15 months. Fruit development requires an additional 5–8 months. Since plant mass at forcing is an important determinate of fruit mass at harvest (Py and Lossois, 1962; Gaillard, 1969; Tan and Wee, 1973; Malézieux, 1988; Malézieux and Sébillotte, 1990b), anything that retards vegetative growth in one season relative to another will either delay harvest or reduce yield.

Seasonal variations in productivity can also be due to the seasonal distribution of rainfall and seasonal and day-to-day variations in forcing success (Wee and Ng, 1968; Wassman, 1991) and in pest and disease pressure. While it is difficult to demonstrate an effect of irradiance on productivity, in Côte d'Ivoire, where temperature is relatively stable and irradiance fluctuates significantly throughout the year, potential plant weight at forcing was correlated with irradiance intercepted during vegetative growth (Malézieux, 1988). In these unirrigated conditions, yield was depressed when drought was prolonged.

DROUGHT AND WATER EXCESS. Because pineapple has a great capacity to survive drought (Sideris and Krauss, 1928), it has been grown successfully on Molokai, Hawaii, in an environment with less than 600 mm $year^{-1}$ of rain (Noffsinger, 1961). Where the soil is well drained, pineapple has also been cultivated in relatively wet areas, such as Guadeloupe, where rain exceeds 3500 mm $year^{-1}$ (Py *et al.*, 1968). Hence, depending on the location and season, the climatic water balance over the crop cycle or some part of it can be largely positive or negative. In Wahiawa, Hawaii, an almost ideal location for pineapple culture without irrigation, pan evaporation averages 1850 mm $year^{-1}$ while rainfall averages 1000 mm $year^{-1}$ (Noffsinger, 1961; Ekern, 1965).

Despite the capacity to survive drought, growth and yield are reduced in all areas where water stress occurs (Foote, 1955; Black, 1962; Ekern, 1964; Py, 1965; Huang and Lee, 1969; Malézieux, 1988). Hence, irrigation or polyethylene mulch or both are regularly used (Hawaii) or are used by some growers (Queensland, Côte d'Ivoire). Though polyethylene mulch has several benefits, its impact on water economy is one of the main reasons it is used in Côte d'Ivoire (Combres, 1983). Several studies report no effect of irrigation on pineapple growth, even where drought occurs (Rao *et al.*, 1974; Tay, 1974; Senanayake, 1978; Htun, 1986). Despite such results, the benefits of irrigation during prolonged drought (Medcalf, 1950; Py, 1965; Huang and Lee, 1969; Combres, 1979, 1983; Kuruvilla *et al.*, 1988; Malézieux, 1992) are sufficient to cause it to be a widely adopted practice. In Guinea, growth of unirrigated plants was delayed by up to 3.5 months by the end of a 5-month dry season (Py, 1965). Despite good evidence of the benefit of irrigation, no quantitative studies were found that would provide the data

needed to predict growth or yield reduction in response to water stress.

In regions of high rainfall, water excess can also limit growth, as well as increasing susceptibility to disease (see Rohrbach and Johnson, Chapter 9, this volume). Waterlogging impedes gas exchange, resulting in elevated CO_2 and depleted O_2 levels in the soil, which lead to decreased growth by inducing root anoxia. In the Mekong delta, for instance, beds may become submerged (Le Van Thuong, 1991), and pineapple plants died after 15 days of submersion of the bed beneath 10–15 cm of water. Where rainfall is high, as in the humid tropics, soils used for pineapple cultivation are generally lower in clay and higher in sand to ensure good drainage. Such soils have low water-holding capacity and are susceptible to erosion (Ducreux *et al.*, 1980; Ciesiolka *et al.*, 1993; El-Swaify *et al.*, 1993; Ciesiolka, 1994). Ridging practices, widely used in South and West Africa and some areas of Australia, also decrease the risk of waterlogging during rainy periods.

Plant growth and fruit weight are decreased by waterlogging that occurs in small field depressions in Côte d'Ivoire. While few quantitative data on the effects of water excess on growth under field conditions were found, until relatively recently, when effective fungicides became available to control *Phytophthora* spp., loss of plants to root and plant rots was a greater concern than reduced growth due to waterlogging (Rohrbach and Apt, 1986; see Rohrbach and Johnson, Chapter 9, this volume).

MISCELLANEOUS FACTORS. Wind is a minor concern for pineapple growers, though prolonged winds have been reported to reduce plant size by 25% (Nightingale, 1942). It is not known if the reduction was due to the physical effect of wind, to an altered water balance or to reduced temperature within the canopy. Though wind has little effect on ET when the plant cover is complete, hot, dry winds, such as the Norte in Mexico or the Harmattan in Côte d'Ivoire, can lead to leaf-tip drying (Py *et al.*, 1987). The influence of wind on thermal exchanges in the canopy is significant (Py *et al.*, 1987). Strong winds cause leaves to rub against each other and the physical damage provides points of entry for fungi (see Rohrbach and Johnson, Chapter 9, this volume), but neither the physical nor the fungal damage is considered economically significant in most instances (Py *et al.*, 1987). Although wind damage is generally minor, wind-breaks of napier grass or sugar cane have been used in some regions of South Africa (Anon., 1956). In coastal areas, wind-borne salt spray can cause burns, leading to blackish spots near the tips of the leaves (Sideris, 1955). Exceptionally strong winds caused by hurricanes can severely damage all parts of the plant or uproot it, leading to significant reductions in yield (Py *et al.*, 1987).

Hail is rare is most areas where pineapple is grown but occurs in southern Queensland (Swete Kelly and Bartholomew, 1993) and southern Africa (Anon., 1956). Hail can seriously damage the rigid and brittle pineapple leaf, significantly reducing leaf area. After a severe hailstorm in Swaziland, most of the leaves wilted and died off, leaving only a small growing point and leading to a loss of 1 year's growth (Anon., 1956).

Few data on the effects of salt on pineapple were found (see Malézieux and Bartholomew, Chapter 7, this volume), but pineapple is grown along windward sea coasts in Hawaii with minimal adverse effects, even though the north-easterly trade winds can be both persistent and strong.

Conclusions

Potential crop dry-matter production depends on the various interacting effects of the physical environment. The complex physiological responses of this CAM plant to several simultaneously varying weather factors (Fig. 5.17) make it difficult to link weather through its effects on physiological processes to dry-matter accumulation, dry-matter partitioning or yield. Even where controlled-environment studies have increased our understanding of physiological responses to one factor, it is difficult to extrapolate such results to the field. These considerations apply to many crops but are a particular problem for pineapple because of

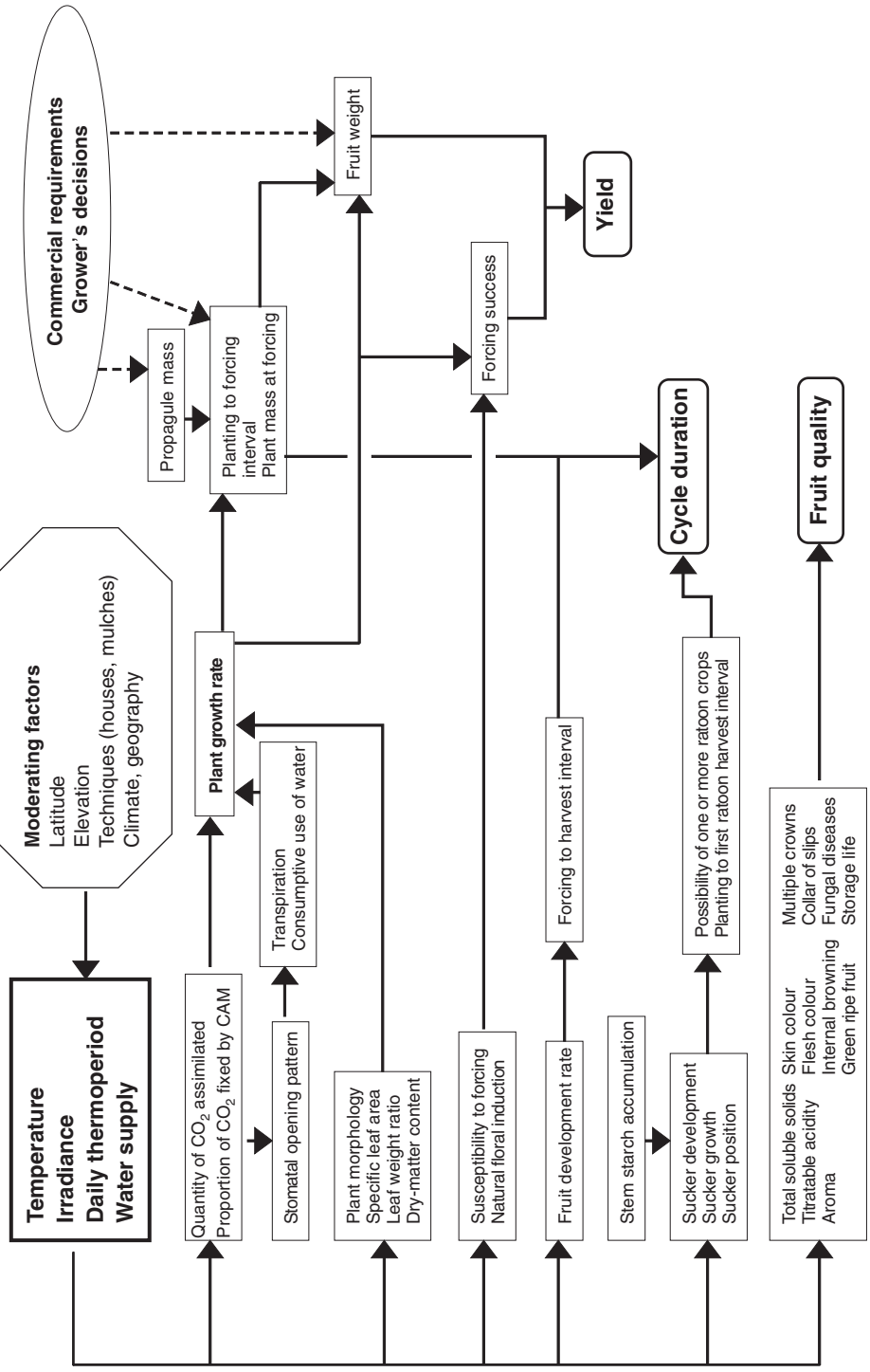

Fig. 5.17. Flow diagram summarizing the effects of environmental factors, but mainly temperature, on pineapple growth and development.

the complex interactions between weather and CAM in carbon assimilation, water economy and growth processes. The effect of temperature on leaf photosynthesis is reasonably well understood, but it is still hazardous to extrapolate this knowledge to the effect of temperature on crop growth. Leaf photosynthesis is apparently saturated at low irradiance, but crop productivity nevertheless seems to respond to total irradiance, as well as to the fraction intercepted by the canopy. This is due in part to the high LAIs sustained at high planting densities. Also, although pineapple has one of the highest WUEs among cultivated crops and can survive severe drought, the reduction in crop growth due to water stress makes irrigation profitable in many areas.

We show here that, despite a significant amount of research on pineapple, it is still difficult to understand and simulate the effects of weather on yield by linking weather variables to physiological processes. There is much opportunity for basic research on pineapple to characterize the effects of irradiance and temperature on carbon assimilation, dry-matter partitioning, reproductive physiology, yield and fruit quality. Only when some of these important issues are resolved will it be possible to understand the complex interactions between weather and physiology. Although prediction of pineapple growth and development as a response to the main environmental factors is now possible in some conditions (Zhang *et al*., 1997), many factors affect the accuracy of such predictions. A comprehensive understanding of the effects of environmental variables on pineapple growth and yield is essential if the accuracy of growth models is to reach the point where it will be possible to satisfactorily predict harvest date and yield. When sufficient data are collected, it may be possible to use growth models to make crop-loss assessments for the several important pest and disease problems that reduce crop productivity.

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6 Cultural System

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Land Selection

General requirements

Temperature

The selection of lands for growing pineapples will most probably be directed by the temperature profile of the areas being considered. Pineapple growth is almost nonexistent below 7°C and above 40°C, so lands where such temperatures occur for long periods of time are unsuitable if production of the crop is to be economically viable. Night temperatures below 7°C are tolerated and may promote flower induction, a sometimes beneficial effect, but freezing temperatures must be avoided.

Growth of leaves reaches a maximum at about 32°C and root growth reaches a maximum at 29°C (Sanford, 1962). The optimum temperature for growth is believed to be nearer a mean of 25°C, with an approximately 10°C diurnal temperature range (Neild and Boshell, 1976). This temperature range will ensure that growth rates are balanced with a sufficiently high rate of net assimilation to ensure that adequate carbohydrate reserves are maintained by the plant, especially near the time of flower induction. While pineapple has relatively high maximum and minimum temperatures for shoot and root growth, the plant is very adaptable and is grown in a very wide area from the Tropic of Cancer to the Tropic of Capricorn, and beyond this area where local temperatures are favourably moderated by unique geographical features. Unique management problems may be encountered when temperatures are considerably below or above the optimum range (see Malézieux *et al.*, Chapter 5, and Bartholomew *et al.*, Chapter 8, this volume).

Topography

Protection of the soil resource from erosion is an important consideration in all agriculture and, for that reason, minimally sloping lands should be selected for pineapple culture. Slopes of no more than a few per cent minimize soil losses, while lands with steeper slopes require expensive drainage channels, contouring and other protective measures to sustain the soil resource.

In the absence of consideration of potential or real soil losses, the limits of topography are usually a result of workers' ability to plant, maintain and harvest the crop. In areas that are exclusively managed with hand labour, pineapples can be grown in fields that are extremely steep (Fig. 6.1), but, where

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mechanization is a requirement for land preparation, maintenance or harvesting, slopes are limited by the requirements of the equipment. Slopes of nearly 40% are farmed with medium-sized machinery in Queensland, Australia, with good results, though erosion losses from such fields can be very high (El-Swaify *et al.*, 1993; Ciesiolka *et al.*, 1995).

Most pineapple-growing areas are laid out with consideration of the impact of rainfall on erosion and drainage. In areas that may experience heavy rainfall or have low infiltration rates, or both, drainage channels should be constructed at intervals that will accommodate the surface runoff and allow this runoff to move off the field with a minimum loss of soil. The details of constructing such drainage channels vary with the characteristics of the soil and the slope of the land (El-Swaify *et al.*, 1982; Hudson, 1995).

Drainage and the removal of water are critical to the successful growing of pineapple, as the root system is intolerant of poorly aerated soils. Areas to be avoided are those that accumulate standing water or that have internal barriers to soil moisture movement, such as plough pans or compacted or impervious soil layers. Where drainage is poor, subsoiling (Fig. 6.2), ripping or installation of internal drainage may be necessary. Ditching and ridging (Fig. 6.3) are used to provide adequate soil drainage where high water-tables exist or where infiltration rates may be low.

Soil types

Pineapples have been grown on a wide variety of soils, from organic peat soils, as in Malaysia, and volcanic ash soils in Hawaii, many Caribbean islands and parts of the Philippines to the very sandy soils found in parts of southern Queensland and northern South Africa. In between are a variety of weathered and secondary-deposit soils, some with forest topsoils and others converted from farm and pasture-lands.

Soils that are ideal for growth have a high organic-matter content with excellent internal drainage and a high soil air content to provide optimum amounts of water, nutrients and oxygen to plant roots. Soils formulated by growers who raised pineapples in the late 1700s in glasshouses in England used a combination of rotted oak leaves, sheep manure, sod and sand, with the proportions being varied by season (Speechly, 1796). Recently, an artificial growing medium, composed of peat moss and vermiculite and fertilized with a complete nutrient solution, has supported outstanding growth of pineapple in a variety of locations worldwide (Hepton *et al.*, 1993). Soil amendments should be selected to improve internal characteristics towards those of the above-formulated media. Soils should have a neutral to acidic pH, although pineapples will grow in slightly alkaline soils if calcium levels are not too high and soil moisture does not favour

Fig. 6.1. Pineapple being grown on steep lands in Hekou County, Yunan Province, China.

Fig. 6.2. Subsoilers used in Queensland, Australia, and in Hawaii, to improve soil drainage (photos courtesy of D. Bartholomew (left) and K.G. Rohrbach (right)).

Fig. 6.3. Ridger used in South Africa to facilitate drainage in heavy soils. Protrusions on the roller establish the plant spacing. (Photo courtesy of Graham Petty.)

the growth of water moulds, such as *Phytophthora* and *Pythium* species.

Sunlight

Pineapple is most productive in areas with extensive sunlight. An ideal climate will have temperatures below 32°C and cloud-free days; however, most climates will have periods of seasonal cloudiness. High irradiance in combination with high air temperatures lead to sunburn, both on the leaves that are directly exposed and on fruit that may lodge at angles that increase exposure. There is no day-length requirement for growth or flowering. The day lengths of pineapple-growing areas near the equator vary less than an hour from winter to summer, while near the tropics of Cancer and Capricorn the variation is somewhat more than 2 h. The variation in irradiance and temperature across the range of latitudes where pineapple is grown has a significant impact on carbohydrate accumulation and subsequent fruit size and yield.

Water

As discussed elsewhere (Malézieux *et al.*, Chapter 5, this volume), pineapple is uniquely adapted to grow well in areas with

low rainfall. The minimum water requirement for unrestricted growth is about 5 cm (2 in.) of water per month; this small amount of water is most efficiently utilized when applied to the root zone in beds covered with an impervious mulch at intervals that will keep the root zone adequately supplied with moisture without loss through excessive application. Where rainfall is less than 5 cm per month, growth will be reduced and either the crop cycle will be lengthened or average fruit weight will be reduced.

Soil surveys

When areas of land larger than 8 ha (20 acres) are being evaluated for pineapple planting, a soil survey should be conducted. A survey will provide important information regarding the topography, soil profile and subsurface variations in soil structure, soil chemistry and drainage. This information will be vital in determining the need for contouring and other erosion-control measures, surface drainage, subsoiling, depth of cultivation, need for bed formation, nutrient requirements and other cultural practices that can be influenced by soil conditions.

The surveys should be conducted by a person familiar with standard survey procedures, including site preparation and soil classification. The survey reports should include any history of past usage, including cropping and soil management. The physical description of the soil by profile should be supplemented with information on physical and chemical analyses to allow appropriate agricultural practices to be developed.

Maps should be prepared that identify boundaries of the growing areas, areas particularly susceptible to erosion, waterways and other drainage channels, roads and pathways, particularly if these are used by the public. The approximate boundaries of each soil type should be identified according to soil classification. All of this information should overlay a topographical map of the area to facilitate development of field layout and drainage systems.

Residential and other environmentally sensitive areas should be identified to facilitate compliance with local regulations.

Soil sampling

A composite sample that adequately represents the soil in the field must be taken so that the results can be used to develop soil-management information for the crop. For the preparation of a composite sample, usually 15–20 core samples are taken in a random pattern from an area of no more than 8 ha (20 acres). Composite samples must be prepared and maintained in a manner that will not compromise the results. Guidelines for sampling and handling soil samples can be obtained from the soil science departments of most universities or analytical laboratories, and analyses can be performed for modest fees.

Where soil surveys show that more than one distinct soil type exists in an area to be farmed, each soil type should be sampled separately if the areas are large enough to be fertilized separately. Areas that are not typical of the general area being sampled should be avoided or, if resources permit, sampled separately. Problem areas should be sampled separately, and additional samples may be required from the subsoil in these areas. Topsoil and subsoil samples should be analysed separately and compared with results from the more typical areas.

Soil analyses

Soil texture

Soil A and B horizons should be evaluated for soil texture. Aspects that can be documented include: (i) coarse fragment analysis; (ii) particle size by hydrometer and hand-sieving; (iii) texture by feel; (iv) moisture content; (v) water-holding capacity (water content at field capacity and at 1.5 MPa pressure); and (vi) bulk density.

Soil pH

Soil pH is measured on a saturated paste. This aspect of soil analysis is important for pineapple culture, as serious problems can be associated with alkaline soils. The most serious is the proliferation of water moulds, *Phytophthora* spp. and pythiaceous fungi, which are parasitic on pineapple roots and

stems. Soils of alkaline pH may also limit the availability of important nutrient elements, with iron being a notable example.

Cation exchange capacity (CEC)

CEC may be estimated using the $NaOAc/NH_4OAc$ replacement method. CEC data provide a measure of the soils' ability to hold nutrients in a form available for uptake by the plant, can have an impact on the frequency of fertilizer applications and may also indicate whether the fertilizer should be applied to the soil or as a foliar spray.

Organic matter

The organic-matter content can be measured by ashing the soil, with the volume of organic matter being estimated from the loss of weight. As mentioned earlier, pineapple plants respond favourably to soils with a high percentage of organic matter. This is not to be confused with crop residue or other organic material that has not undergone complete decomposition by composting or other means that result in a stable C/N ratio in the soil.

Total elemental composition

Soil elemental composition can be measured by $HNO_3/HClO_4$ digestion and analysis by inductively coupled plasma (ICP) spectrometry. Metals analysis can be made for Fe, Zn, Cu, Mn, Cd, Cr, Ni and Pb and the water-soluble elements Ca, Mg, Na, K, S and B can be determined.

Nitrogen in the soil can be measured by the Kjeldahl method. Not all soil nitrogen is fully available, though mineralization gradually releases nitrogen in organic matter. Nitrogen in the mineral form should eventually be replaced to maintain an adequate supply for plant nutrition.

Land and Soil Preparation

Land clearing, field layout and bed design

If the site has not been cropped previously, the first operation will probably be to remove brush and trees. After the fields have been surveyed to establish the slope, need for and frequency and position of drainage channels, these channels should be installed so as to effectively capture and remove excess rainfall in a manner that minimizes erosion. If drainage channels discharge into adjacent waterways, the need for permanent drop structures should be evaluated.

Where rock removal is necessary, rocks larger than about 30 cm (1 ft) in diameter should be removed after ploughing or subsoiling and after final land preparation. Rock removal from stony fields can be expensive and, in some cases, specialized equipment has been developed to mechanize the removal process (Fig. 6.4). These rocks may be used for construction of drop structures or other field construction or, if excessive, they may be left in piles.

In areas where field operations are machine-assisted, planting areas may be laid out in blocks separated by roads. The dimensions of the blocks are designed to accommodate the equipment, while effectively accomplishing the required field operations. Where boom sprayer equipment is to be used, block size is usually twice as wide as the spray boom is long.

Once the basic tillage operations (Fig. 6.5) have been performed, raised planting beds may be formed (Fig. 6.3) if there are known economic advantages. In most cases, pineapple plant growth is enhanced by planting on raised beds due to the increase in the volume of topsoil available to the root system, enhanced aeration and superior drainage. Raised beds may or may not be covered with plastic mulch, usually depending on the need for fumigation. In some cases, where capture of sparse rainfall is important, slightly depressed beds direct limited rainfall or overhead irrigation to the planting line. Despite the advantages of raised beds, they are not used where the cost of preparation exceeds the economic benefit.

Treatment of previous crop residues

Knock-down and incorporation

Because of its leaf morphology and succulence, pineapple plants are slow to desiccate,

Fig. 6.4. Rock picker used in northern Queensland, Australia, to remove large rocks from pineapple fields prior to planting (photo of Duane Bartholomew).

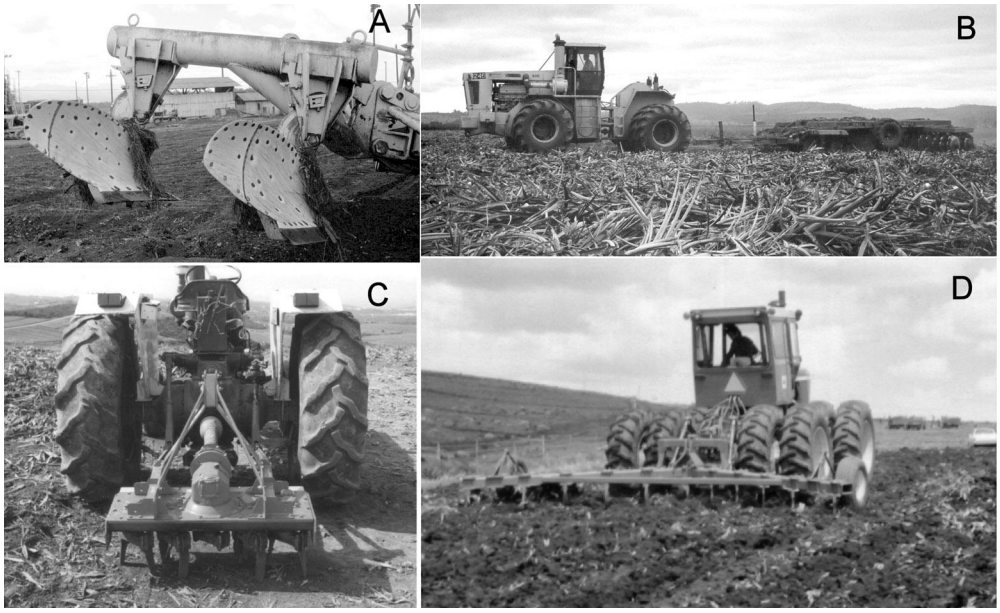

Fig. 6.5. A, Large mouldboard plough used in Hawaii to incorporate dried plant trash; B, four-wheel-drive tractor and heavy disc used for primary preparation after ploughing (photo courtesy of CAMECO Corp.); C, rototiller used to improve soil tilth after primary tillage operations (photo courtesy of Graham Petty); D, spring-tooth harrow used for land preparation in South Africa (photo courtesy of Graham Petty).

and shoots produced from living plant stems incorporated into the soil can be a serious weed in fields. Thus, it is common to chop standing plants by discing or power flail to hasten their desiccation and decomposition. In the peat soils of Malaysia, plants are killed with gramoxone to hasten their desiccation. Once desiccated, plant residues may be

burned under dry conditions or incorporated into the soil, provided there is sufficient moisture and time for decomposition.

Pineapple plant residue may also be harvested for animal feed or for by-products, such as fuel, fibre or extracts, such as the enzyme bromelain. Removing the crop residue may help to shorten the crop intercycle for timely production schedules. However, repeated removal of pineapple residue depletes the soil of essential nutrients and organic matter. Soils with poor structure, low native organic matter and low CEC benefit most from residue incorporation and are most adversely affected by residue removal. The benefits of residue incorporation can accrue over several crop cycles. Well-aggregated soils with a stable organic-matter fraction and a comprehensive supply of nutrients may show little benefit from residue incorporation, at least in the short term.

Conventional tillage

Poor tilth and impediments to drainage are especially unfavourable to pineapple. The chief objective of tillage is to achieve excellent soil tilth to improve contact with the planting material and for rapid and sustained root development. Tillage should achieve a permeable soil profile that is free of rocks and large clods and a homogeneous distribution of decomposed residue, amendments and fertilizers. Where fumigation for nematode control is essential, fine tilth must be achieved for effective distribution of the fumigant.

Compaction due to residue management, tillage operations and in-field traffic may easily become counterproductive. Compaction needs to be avoided or minimized by selecting the right equipment according to soil type, internal soil structure, soil moisture, organic-matter content and the time available to prepare the land.

Subsoilers are used to break up impervious or compacted internal layers to improve drainage without changing layering of horizons in the soil profile (Fig. 6.2). Deep ploughing may be used where mixing or redistribution of nutrients or soil layers results in an improved planting and growing environment. Harrows and discs (Fig. 6.5) are used to break up clods to provide a suitable tilth for planting. Rollers, cultipackers, rototillers and levelling boards may be used to finish the tillage operations. These operations will be followed by bed-forming, preplant fertilizer application and fumigation, with mulch laying, where these operations are appropriate.

Minimum tillage

The practice of minimum tillage is becoming increasingly popular because it can reduce the cost of land preparation, conserve organic matter from the previous crop, reduce moisture loss during land preparation, preserve the balance of microflora and microfauna in the soil profile and reduce soil erosion. However, there may be valid reasons for not using minimum tillage. For example, tillage may be necessary to facilitate the control of ants and mealybugs, which are intimately associated with mealybug wilt, and excellent tilth is essential to good distribution of soil fumigants used to control nematodes. In some soils, tillage may be necessary to provide tilth that will allow planting.

In those soils where tillage is not a prerequisite for subsequent operations, the previous crop residues may be physically or chemically killed and allowed to form an organic mulch through which the pineapple plants are planted. If minimum tillage practices are used, special consideration should be given to plant nutrition. Preplant incorporation of plant nutrients may not be possible and the plant nutrients may not be uniformly distributed in the root zone. These limitations may place a greater burden on timely application of foliar and soil-applied nutrients.

Soil amendments and fertilizers

Soil amendments, such as lime and organic matter, influence plant growth indirectly by improving the physical or chemical condition of the soil, though amendments gener-

ally also provide plant nutrients. Composted animal manures provide organic matter and improve soil structure, while supplying plant nutrients. Lime adjusts soil pH, as well as supplying calcium, and, if from dolomite, it also supplies magnesium. Pineapple root development can vary dramatically among locations, so a site-specific understanding of root development is important to determine whether or not plants will respond favourably to the use of soil amendments. Soil amendments can be broadcast immediately after knock-down so that they can be incorporated by tillage operations. Preplant fertilizers can be banded just below or adjacent to the plant line during bed formation to allow early interception by the developing roots.

Ideally, amendments and preplant fertilizers should provide all the needed nutrients in conjunction with side-dressing or foliar fertilization, or both, while maintaining a good soil tilth, which will encourage a healthy root system. For best results, nutrient management for pineapple should begin with soil sampling prior to land preparation and continue until floral differentiation. Various nutrient-management strategies are discussed later in this chapter.

Mulches and fumigants

Vapour-barrier mulches have several beneficial effects, but the primary benefit is to retain soil fumigants. Early mulches were made of heavy craft paper impregnated with materials to slow its decomposition. More recently, thin plastic mulches (Fig. 6.6) that contain inhibitors to slow degradation by ultraviolet light are being used. These mulches also inhibit weed growth, retain soil moisture, raise soil temperature and can be marked with guides to allow precision planting. To assure proper plant densities, sample lots of mulch should be evaluated after laying in the field to determine the amount of stretch that occurs during application.

Planting Material

General requirements

A wide variety of vegetative material can be used to propagate pineapple plants (Fig. 6.7). The more common ones are: crowns from the top of the fruit; slips from the peduncle directly below the fruit (these pieces usually have a rudimentary fruit or knob at their

Fig. 6.6. Pineapple field mulched with black polyethylene plastic in Hawaii. Note marks used to establish plant spacing.

base); hapas, which are borne lower on the peduncle; suckers, which originate on the upper part of the stem; and ground suckers, which form on the lower part of the stem with roots that grow into the ground while they are still attached.

Other planting material may be generated by sectioning parts of the plant or by destroying the apical growing point of vegetative plants, stimulating growth of lateral buds. Both methods produce what are usually called plantlets. Plants in the process of flower initiation may be treated with such chemicals as Maintain CF125 (chlorfurenol), which stimulate the production of slips and crownlets, also called propagules.

Comparisons of various types of planting materials show that early growth rate and plant size at some future time are influenced primarily by the amount of starch reserve in the piece, the amount of leaf material present and the freshness of the piece of material. These variables have rarely been well controlled in field trials comparing various types of planting materials; consequently there remains some controversy over the relative performance of types of planting material. Some practical aspects of the various types of material are given below.

Crowns

Large quantities of crowns can easily be gathered with fruit being harvested for processing. They can be inexpensive and, if planted fresh, perform well if protected against heart and butt rot with fungicides. Equipment is available that allows for the treatment of planting material with pesticides at the time of harvest. Crowns are usually not available where fruit are produced primarily for the fresh market, because the fruit is marketed with the crown. Also, crowns are unsuitable as planting material if the growing point has been gouged in an

Fig. 6.7. Pineapple planting material can be obtained from the fruit crown (top right), slips (top middle) or suckers (top left), or from sectioned crowns (middle) or stems (lower) when labour is available or there is a need to rapidly increase the supply of available planting material.

attempt to increase fruit weight by limiting crown growth during the latter phases of fruit development.

Slips and hapas

These shoots are similar in origin in that they develop on the peduncle from the differentiation of lateral buds during fruit initiation. However, they are quite different in shape because slips grow outward and then upward around the base of the fruit, resulting in a sharp curvature at the base of their stem. Hapas emerge well below the fruit and have the same 'arrow' shape as suckers initiated lower on the stem. Slips and hapas are usually left on the plant for several weeks after fruit harvest and a separate harvesting operation is needed to collect them, so these propagules are more costly than crowns. Not all pineapple varieties develop slips, but when they are present in large numbers, they reduce average fruit weight and yield (Collins, 1960; Wang and Chang, 1960).

Slips are a good source of planting material, but large knobs should be removed before planting, as they may rot in the soil and lead to rot of the stem piece under wet conditions. The performance of slips, in terms of months from planting to harvest, is generally intermediate between crowns and suckers, probably because they are generally intermediate in size between the smaller crowns and larger suckers.

Suckers

Suckers are grown on the plant for a few to several weeks after fruit harvest, and harvesting is fairly labour-intensive because the suckers must be cut from the plant. In Thailand, suckers are the preferred planting material by small farmers, because the Thai clone of 'Smooth Cayenne' produces few or no slips and most farmers gouge the crowns to increase fruit weight. Suckers can be gathered, stored and shipped without much loss of vigour and, because they can be large (up to 1.5 kg), they can reach forcing weight in a shorter time than slips or crowns. A particular problem with suckers is that they may have undergone floral differentiation before they were harvested or the shock of harvesting and storing may have induced differentiation. Because these plants do not grow before floral differentiation, a small fruit is produced on a small plant.

Plantlets

Plantlets are usually produced where rapid propagation is the objective. Plantlets may be grown from the sectioning of plant material, by decapitation (Heenkenda, 1993), also called gouging, or from tissue culture.

Sectioning

Any vegetative shoot of the pineapple plant can be sectioned for propagation if the pieces have two or more axillary buds and some leaf material (Fig. 6.7). For large stems, the leaves are cut off, the stems are quartered lengthwise and each piece is then cut into sections 3–5 cm in length. A small amount of leaf material is usually left attached to each piece. The sections are cured by drying, or treated with fungicide, or both, and planted in a well-prepared nursery. The soil in the nursery should be fertile at the time sections are planted or the new shoots can be fertilized by foliar feeding with a dilute nutrient solution.

Crowns may be similarly microsectioned, producing four or more sections per crown. When such small sections are produced, they are best planted in sterile media and grown in the greenhouse. Small crown sections should be started in a well-drained medium, such as coarse sand, and must be kept moist. When using a medium of low native fertility, foliar feeding should commence soon after the new shoots emerge.

All material produced from sections must be grown to an adequate size for field planting and hardened if they have been grown under shade or greenhouse conditions. Plantlets may develop rapidly in the field if they have a well-developed root system at the time of planting.

Gouging

Gouging is the mechanical removal of the shoot apex of growing plants, usually with a tool specifically designed for the purpose (Heenkenda, 1993). The young leaves are pulled out prior to gouging. Gouging destroys the plant's apical dominance, thus releasing axillary buds from their induced dormancy. These buds form shoots, which, when large enough, are harvested and planted in a nursery or field.

Plants as small as 100 g have been gouged, but such small plants would normally be gouged in a greenhouse with fine tools. When gouging is done in the field, plants should be larger so that the gouging can be done by workers from a standing position. The gouge should be shallow, preferably not more than about 1.0 cm below the apical bud. Treatment of the gouged plants is necessary to avoid rot. Shoots produced after gouging are allowed to grow to the desired size and their mass at the time of removal depends on the conditions under which they are to be planted. Very small plants, less than 50 g or so, would normally be planted in a greenhouse under shade. Plants weighing between 50 and 100 g could be planted in a propagation bed in the field, while plants weighing 200 g or more are suitable for use in establishing commercial plantings. A well-maintained mother-plant nursery can be productive for 8–12 months, after which it can either be rejuvenated or knocked down and replanted. Rejuvenation involves allowing at least one low-attached shoot to grow until it is of gouging weight. When expanding clones, great care must be exercised to keep the area free of pests and diseases, as the material is the foundation stock for the farm.

Tissue culture

Propagation by tissue culture is discussed in detail by Smith *et al.*, Chapter 4, this volume.

Propagules

Propagules are usually developed by chemical stimulation of the plant during differentiation, so these pieces of planting material most resemble crown or slips. Plants are forced following normal farm practice and then treated with a solution of up to 400 p.p.m. chlorflurenol in 3000 l ha^{-1} within a few days after forcing (Py *et al.*, 1987). Propagules usually develop in place of the fruit, or the fruit are deformed so that the fruit are unusable after this treatment. With proper timing and chlorflurenol concentration, up to ten good-sized propagules can be produced on each plant. Propagules should be carefully graded by size before planting, and plants from different production areas should not be mixed if field uniformity is to be maintained. Propagules are an important type of planting material in fresh-fruit operations where crowns are sold with the fruit and slip or sucker harvesting is too expensive or inadequate to fulfil planting-material requirements.

Treatments before planting

All planting material is subjected to a variety of treatments prior to planting. These include curing, bundling, transportation from the field or growing area, grading, storing, dipping, transport to the planting field, spreading and finally planting. These treatments will not all be discussed in detail, as practices vary with the areas in which the pineapples are grown. However, the important points are covered in the following paragraphs.

Planting-material size and uniformity are particularly important. Within any category of planting material, large pieces will usually grow to forcing weight faster than smaller pieces generated in the same area. For this reason, grading of planting material by size is critical to provide uniform plants at forcing and efficiencies at time of harvest.

Crowns, slips, hapas, suckers and propagules are very tolerant of storage and may be stored for months between harvest and planting. However, stored plants continue to grow, stem diameter decreases and storage reserves are consumed, so prolonged storage slows initial growth and increases variability (Py *et al.*, 1987). Therefore, fresh planting material is almost always superior to stored

material because it grows faster. However, very fresh material should be treated with a fungicide to avoid black rot caused by *Chalara paradoxa*. Dipping of plant material is done to protect against rots and control pests. For details on control of pests and diseases of planting material, see Rohrbach and Johnson (Chapter 9, this volume).

Storage of planting material should be under conditions that allow for good air movement to avoid rot. Storage in piles or other conditions that block exposure to light should be kept to a minimum, as stem etiolation will occur if the material is deprived of light for more than 2 weeks.

Spreading of planting material in the field should be done to facilitate the work of planters and to provide the appropriate amount of planting material for the areas assigned to be planted (Figs 6.8, 6.9). Oversupply should be kept to a minimum, as additional handling can damage the planting material and it will not perform as well as material only spread once.

Fig. 6.8. Distribution of planting materil in the field with a tip trailer in South Africa and with a boom in Hawaii. (Photos courtesy of Graham Petty (left) and K.G. Rohrbach (right).)

Fig. 6.9. Hand-planting of 'Smooth Cayenne' pineapple. Pineapple planting material has been spread to speed the planting operation.

Planting

Planting density

Many factors are involved in the determination of planting density and, as a result, densities may vary from as low as 29,000 plants ha^{-1} (12,000 plants $acre^{-1}$) to as high as 86,000 plants ha^{-1} (35,000 plants $acre^{-1}$). Both environment, especially solar radiation, and nutrition influence plant growth and the competition between plants for available resources. Marketing is an important consideration for the grower, because plant growth rates and plant size at the time of forcing influence fruit weight and fruit-size distribution. Densities are selected to manage these relationships with a view to effecting the desired production.

Sunlight intensity and duration determine the amount of energy available for photosynthesis. Areas with long periods of cloud-free days will support greater carbohydrate assimilation than will cloudy areas. Seasonal variations will be more accentuated in those growing areas farther away from the equator. Where seasonal changes are large, density changes on a seasonal basis may need to be considered for optimum production.

Experiments conducted on the effect of density on average fruit weight and yield have shown quite predictable results. Average fruit weight decreases linearly with increasing density, but the effect is variety- and site-specific (Fig. 6.10). For 'Smooth Cayenne' in Hawaii, fruit weight decreases by 2.4% per 1000 increase in plants per acre over a wide range of densities. Total yield per unit land area generally increases curvilinearly with increasing density (Fig. 6.11), though some studies show that yields decline at very high plant populations. Typical plant population densities for 'Smooth Cayenne' range from about 60,000 to 80,000 plants ha^{-1} (24,000–32,000 plants $acre^{-1}$). The optimum density for a given farm or region and variety must be determined by the available technology, environmental resources and market requirements.

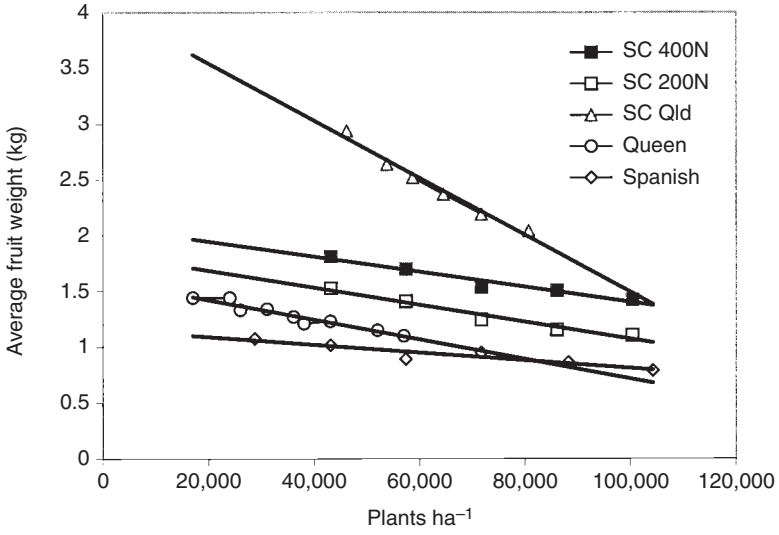

Fig. 6.10. Effect of plant population density on average pineapple fruit weight of 'Queen' grown in Ghana (Norman, 1978), 'Singapore Spanish' grown in Malaysia (Wee, 1969) and 'Smooth Cayenne' grown in Queensland, Australia (Scott, 1992), and Swaziland (Dodson, 1968). Regressions are 'Queen', $y = -9 \times 10^{-6}x + 1.59$, $R^2 = 0.93$, $n = 9$; 'Singapore Spanish', $y = -3 \times 10^{-6}x + 1.16$, $R^2 = 0.835$, $n = 6$; Queensland 'Smooth Cayenne' ($y = -3 \times 10^{-5}x + 4.05$, $R^2 = 0.98$); Swaziland 'Smooth Cayenne', 400N, $y = -6.8 \times 10^{-6}x + 2.08$, $R^2 = 0.95$; 200N, $y = -7.6 \times 10^{-6}x + 1.84$, $R^2 = 0.96$, $n = 5$, where y is estimated fruit weight in kg and x is plants ha^{-1}.

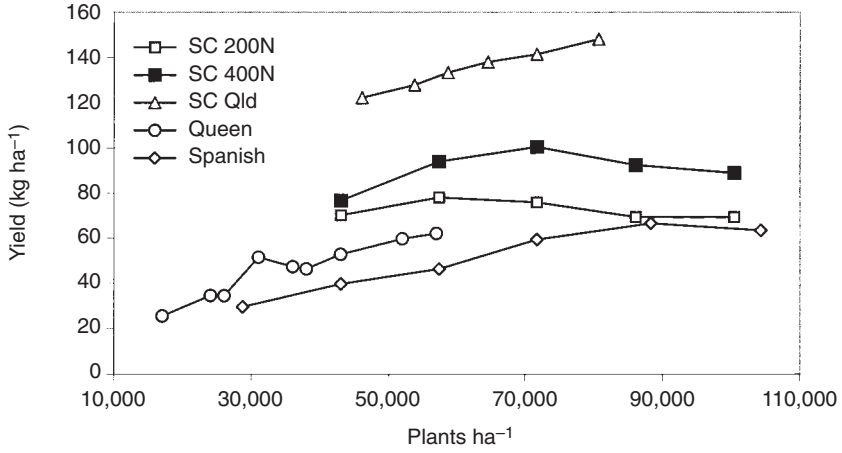

Fig. 6.11. Effects of plant population density on pineapple fruit yield as shown by the authors or calculated from their average fruit-weight data. Data are for 'Queen' grown in Ghana (Norman, 1978), 'Singapore Spanish' grown in Malaysia (Wee, 1969) and 'Smooth Cayenne' grown in Queensland, Australia (Scott, 1992), and Swaziland (Dodson, 1968).

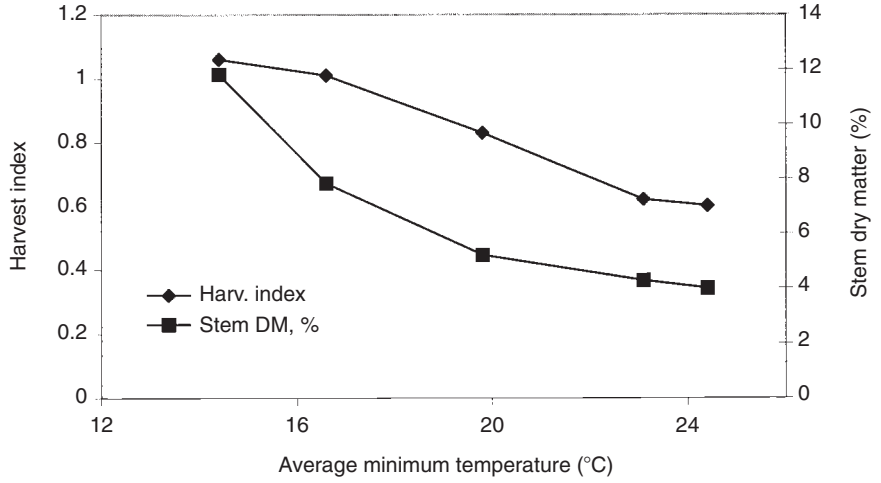

Fig. 6.12. Effect of average night temperature on stem dry matter (DM) content as a percentage of total plant dry matter and on fruit harvest index calculated from plant fresh weight at forcing and fruit weight at harvest (redrawn from Hepton *et al.*, 1993).

Ratios of fruit mass at harvest to plant mass at forcing (harvest index) have been measured in various regions where pineapple is grown. The harvest index can be as low as 0.4 in areas with warm nights and fast growth rates and can exceed 1.0 where irradiance is high and night temperatures are cool. Where growing medium and nutrition were controlled in a variety of climatic conditions (Hepton *et al.*, 1993), stem dry-matter content as a percentage of total plant dry matter and harvest index decreased as average night temperature increased (Fig. 6.12). Thus, stem dry-matter content has a strong influence on the harvest index of 'Smooth Cayenne' pineapple (Fig. 6.13). These factors should be taken into consideration when selecting a planting density.

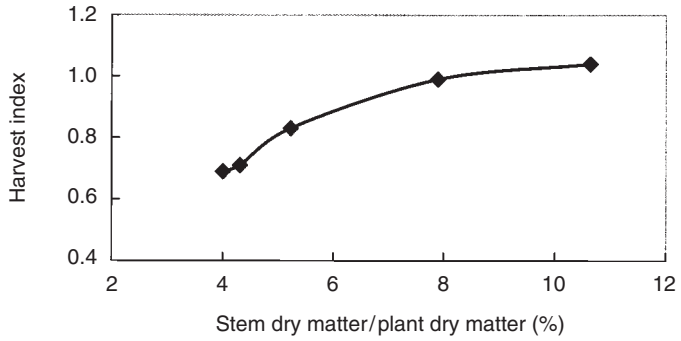

Fig. 6.13. Effect of stem dry-matter content on harvest index calculated from plant fresh weight at forcing and fruit weight at harvest (redrawn from Hepton *et al.*, 1993).

Plant arrangement

Plants can be arranged in the field in single rows or in beds of two, three or four rows. The spacing between plants in the row and between rows is determined by the desired plant population density, type of planting material, planting methods, use of plastic mulch, use of raised beds, methods of plant fertilization and methods of harvesting. One of the more usual arrangements involves two-row beds with an adequately wide walk space between the beds to allow for field activities, particularly harvesting. In this scenario, the distance between the plants within a line, which should not be less than about 20 cm (about 8 in.), is less than the distance between the lines in the bed.

The density used is generally determined by the variety or clone being planted, the intensity of cultural practices used and the planned use of the fruit. Planting densities of less than about 50,000 plants ha^{-1} are common in market gardens or where clones with long, spiny leaves, e.g. 'Singapore Spanish' or 'Red Spanish', are grown (Py *et al.*, 1987). Densities for 'Smooth Cayenne' are typically between 50,000 and 75,000 plants ha^{-1}. Currently, higher densities typically are used where fruits are destined for the cannery and lower densities are used where fruits are marketed fresh. Fruit for the fresh export market should weigh between 1.7 and 2.5 kg, requiring an overall average fruit weight of 1.9 kg, while fruit recovery in the cannery is highest if fruit weigh about 1.6 kg, because recoveries are highest when fruit fit standard No. 2-size cans (J. Gonzales, 2002, personal communication).

Planting depth

An important aspect of planting is obtaining good contact between the planting material and the soil. Where labour is not expensive, basal leaves and knobs on slips can be removed by hand to expose adventitious roots, facilitating good contact with the soil. Good soil tilth and plant setting also contribute to an early and uniform plant start. Placing planting material sufficiently deep into the soil is one of the most effective ways of assuring a good plant start.

Crowns, propagules and plantlets are most sensitive to deep planting, but even these can have half of their height buried at planting without adverse effect. Protection of these planting materials against heart rot is necessary in soils with poor drainage and where soil pH is above 5.5 and thus conducive to the growth of water moulds.

Slips, hapas and suckers may be planted to depths of 10–15 cm (4–6 in.) without adverse effect. Also, no benefits will be obtained from the removal of basal leaves if the soil has a fine tilth and adequate provisions are made to move the soil – for example, with setting irrigation – into the lower leaf axils.

Mechanical planting

Driven by the high cost of labour in some pineapple-growing areas, a variety of planters have been developed to plant pineapples (Fig. 6.14). These machines usually work best in fields that do not require mulch. Such machines usually involve placing the planting material in a holder that will deposit it into a prepared hole or furrow. Planting material may be set by compression wheels that follow immediately behind or by rolling plants after planting (Fig. 6.15). The quality of planting is often not as good as with hand-planting and machines that automate the planting process tend to damage the growing point of the planting material. In addition, machines usually require exceptionally good tilth to meet minimum expectations for planting quality. Under these ideal planting conditions, hand-planting is usually faster and better than machine planting under average conditions of land preparation.

Attempts to plant with mulch, using machines, have been only marginally successful and no such planters are currently known to be in use. Fumigation is usually done at the time the mulch is laid. The use of additional

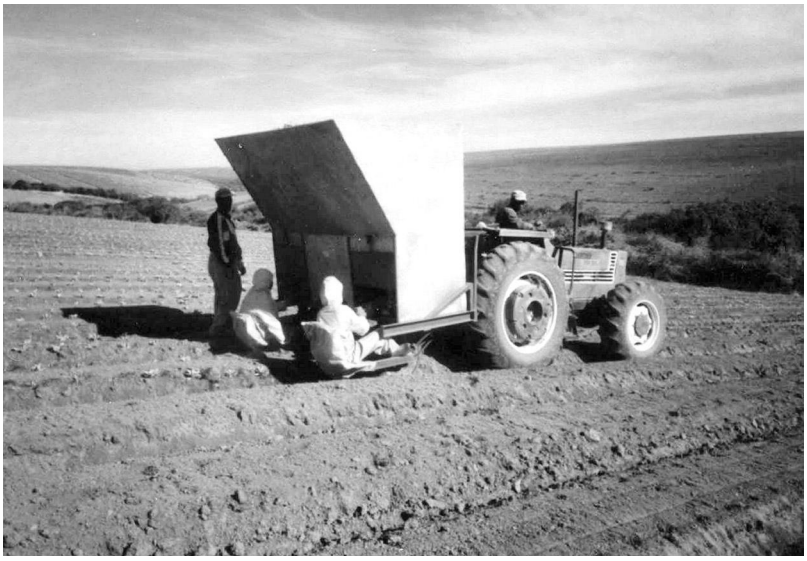

Fig. 6.14. A relatively simple pineapple planter used on a pineapple farm in South Africa (photo courtesy of Graham Petty).

Fig. 6.15. Setting plants by rolling on a pineapple farm in South Africa and by overhead irrigation in Hawaii (photos courtesy of Graham Petty (left) and K.G. Rohrbach (right)).

workers to manage the fumigation operation and handle planting material increases the risk of worker exposure to the fumigant, even with the required protective clothing. Planting through mulch that is already in place presents another barrier to deal with that is not present in unmulched fields.

Setting

To obtain good root initiation, uniform levels of moisture and aeration must be developed in the rooting zone of each piece of planting material. Too much moisture without aeration leads to rot, while too little moisture leads to uneven root initiation and variability in growth start and subsequent development.

Good tilth is a prerequisite for good rooting, as it allows fine soil particles to be moved around the base of the planting material. Soil can be moved by hand, with the planting tool, by foot (often the heel of the planter), by rolling, as is practised by some in Australia and South Africa, or with irrigation (Fig. 6.15).

Setting with water has a dual effect. Water moves the soil particles around the base of the planting material, but, in addition, provides water for subsequent plant growth. In arid growing areas, this setting irrigation must be supplemented by timely additional rounds of irrigation to sustain the root growth.

Volumes of water used in setting irrigation depend on the method of application, the soil moisture levels at the time of application, the use of mulch material and soil conditions. A usual quantity would be about 5 cm (2 in.) by direct overhead application, or somewhat less if by drip irrigation. Drip irrigation does not move soil particles to any degree, but if the soil tilth is adequate, irrigation may enhance plant–soil contact sufficiently to allow uniform root initiation.

Water Requirements and Irrigation

Determination of water requirements and plant moisture status

While the pineapple plant is a xerophyte and is capable of good crop production under relatively low water regimes, the plant responds well to as much as 5 cm (2 in.) of water per month from rain or irrigation (Fig. 6.16). Maintaining readily available soil moisture in the immediate root zone requires less water for pineapple than for other crops that have much higher transpiration rates.

The entire pineapple plant adapts to drought and thereby maintains a productive potential in dry soil. Pineapple roots survive drought by suberization, a survival mechanism that limits their capacity to explore the soil for nutrients and moisture. Drought also results in the closure of stomata during the entire day (see Malézieux *et al.*, Chapter 5, this volume). However, plants that are grown under ample moisture in well-aerated soils have well-distributed roots with numerous white root tips. This enhances the consumptive use of water and carbon fixation, an adaptive feature that is partly responsible for the exceptional response that

Fig. 6.16. A, Drip-irrigation system used in dry areas in Hawaii; B, self-propelled overhead irrigator used where drip irrigation is unavailable.

pineapple shows to drip irrigation (Fig. 6.16A).

While much of the world's pineapple is grown without irrigation, long periods of inadequate rainfall seriously compromise both plant growth and fruit development. In the drier areas of Hawaii, irrigation was a necessity if predictable yields were to be obtained. Soil and leaf moisture readings have been used to develop guidelines for irrigation scheduling. Once the guidelines are understood, rainfall can be considered in the scheduling. Because all areas cannot be irrigated simultaneously on a large plantation, irrigation is usually scheduled to begin before it is actually needed in the most sensitive areas. These are usually young plant-crop fields. Irrigation is completed after the ideal time in the older ratoon fields, where the crop canopy minimizes soil drying and associated moisture loss.

The pineapple leaf is a major water-storage organ for the pineapple plant (see Coppens d'Eeckenbrugge and Leal, Chapter 2, and Malézieux *et al.*, Chapter 5, this volume). The cells of the upper mesophyll layer can occupy almost 50% of the leaf volume when full of water. Under conditions of limited water-supply, the water in the mesophyll layer is withdrawn by the plant. The subsequent shrinkage of the leaf thickness can be used as an indicator of water deficiency. In practice, representative 'D'-leaves are pulled, nested together in a group of six to ten leaves and the total thickness is measured and compared with the thickness of fully turgid leaves.

A shortcoming of this method is that it does not take into account the viability of the root system and its ability to extract moisture from the soil. Roots infested with nematodes or symphylids, damaged by grubs or diseased with fungal pathogens may result in leaves showing moisture deficit, while soil moisture is sufficient for a healthy plant.

Overhead irrigation

In Hawaii, overhead booms (Fig. 6.16B) were found to be the most effective way to saturate dry soil and initiate root growth after planting by using about 5 cm (2 in.) of water. The same overhead booms could be used to irrigate growing plants, usually applying 2.5–5 cm (1–2 in.) per month. The booms travelled directly above the planted areas and only applied water at a rate that could be absorbed by the soil with each pass. On the island of Lanai, Hawaii, pineapple was planted through mulch in depressed beds, which helped direct the water to the roots. Other forms of overhead water application have been used with good effect but the irrigation efficiency (water applied/water available to the crop) is generally not as high as it is with the overhead boom.

Drip irrigation

While the high initial investment associated with drip irrigation may appear prohibitive for pineapple culture, in areas where water is limited or expensive and the need for irrigation may extend for many months, the investment will pay good dividends. Drip irrigation allows precise placement of water in the root zone in volumes that match the crop's consumptive demand. Drip irrigation is especially effective during the first few months after planting, when a consistent but low-volume supply of water is needed for the developing root system.

Drip-irrigation systems involve the following major components: a water source, a filtration system if particulate matter that can clog emitters is present, chlorination to prevent microbial growth in the drip tubes, a system of in-field distribution pipes, which bring water at the correct volumes and pressures to various parts of the fields, and the emitter tubes, which are usually buried just below the soil surface between two lines of plants.

The emitter tubes are usually custom-made for pineapple to allow for a slow release of relatively low volumes of water. If the soil has good hydraulic conductivity, the slow release results in wider spreading of the water in the root zone. Flow rates will depend on orifice spacing, orifice diameter and line pressure, and these variables will depend on the soil type and cost and avail-

ability of water. The length of run for emitter tubes will depend on the slope of the terrain, but should be limited to lengths that will result in output variations along the tubes of no more than 10%. As with overhead irrigation, scheduling includes a consideration of rainfall, with the younger plants taking precedence over the more established ones.

Drip irrigation may be used to safely deliver water-soluble fertilizers, nematocides and fungicides to the root zone. However, drip irrigation does not guarantee the desired effects from these materials, as their dispersal and reaction in the soil are largely uncontrolled and may not be as well understood when compared with the standard methods of application. For example nitrogen is easily leached with excess irrigation and, like other nutrients, is recovered by the crop according to the distribution and vigour of the roots.

Weed Control

The requirements for effective weed control in pineapples vary considerably in various parts of the world. Weed-control practices are not reviewed here, but weeds should be controlled so that they do not seriously impede crop growth or compromise harvesting and other key operations. Special attention should be paid to the reduction and elimination of clump grasses and vines, as these can become extremely problematic.

The pineapple plant is quite tolerant of many good herbicides, particularly in the few days immediately after planting and before root initiation. This is an ideal time to apply pre-emergence herbicides. In Hawaii, bromacil, hexazinone, ametryne, diuron and quizalofop-P-ethyl are registered for use on pineapple and are used alone, or they may be combined within limits provided by the registration label to control a broader spectrum of weeds and prevent one weed species from becoming dominant. The solubility and persistence of bromacil and hexazinone make them prone to leach to groundwater in permeable soils, so the environmental hazards section of the product label includes a groundwater advisory about their use in such soils. The use of mulches will also effectively block weed growth in the planting bed, where mulch can be justified for other reasons, such as soil fumigation, moisture retention, temperature control and conservation of soil and nutrients. For additional information related to weeds, see Rohrbach and Johnson, Chapter 9, this volume.

Plant Nutrition

Assessment of nutritional requirements

Pineapple responses to nutrient management are dramatically affected by the condition of the soil and the health of the developing root system. Pathogens, nematodes, waterlogging and impermeable soil easily inhibit the crop from assimilating nutrients and responding to fertilizers. Indeed, several symptoms due to stress in pineapple are easily misinterpreted as nutritional deficiencies. When optimum growing conditions prevail, particularly for the roots, significant economical responses can be achieved with both soil-applied and foliar-applied fertilizers.

A preliminary assessment of nutrient requirements can be made by soil testing. Soil samples should be taken prior to land preparation, such as just before knockdown, and should represent the rooting volume of the native soil, less any contributions made from the crop residue. The total nutrient-management programme for pineapple is determined for three important stages – broadcast amendments for soil improvement, localized preplant fertilizer to promote early rooting and early nutrient uptake, and postplant side-dressing or foliar fertilizers for the remaining nutrients which may still be limiting. Such a composite fertilizer programme has great flexibility and provides for maximum economic benefit. A variety of total nutrient-management programmes exist for pineapple, given the diverse environments and the range of available fertilizers. Moreover, fertilizer programmes in successful farms are usually under constant evaluation to discover opportunities for additional responses.

Broadcast amendments

Broadcast amendments are applied prior to planting to adjust soil pH or to increase the supply of Ca, K, N and P. Rock-phosphate, lime, animal manure and well-composted organic material have all been used successfully in pineapple culture systems under the right conditions. Benefits from broadcast amendments should not be assumed; thus, diagnostic soil testing is needed to verify specific deficits, such as soil pH (for lime), Ca and K (for lime and manures) and P (for phosphates).

Amendments must be broadcast uniformly and incorporated to the desired depth to provide the most benefit for the developing root system. Major problems can arise when soil amendments are not applied and incorporated uniformly. Among the serious problems is a localized high pH, which favours the infection of susceptible pineapple plants by *Phytophthora* and *Pythium* fungi (see Rohrbach and Johnson, Chapter 9, this volume). When manure is used, extreme care must be taken to avoid adverse effects in areas where the manure is temporarily stored in the field before spreading, or where spreading is not uniform and the quantities applied exceed desirable levels. Salts leached from cattle manure can severely restrict growth. Similarly, high soil pH resulting from the application of chicken manure or coral scraped from feedlot sites has led to spotty outbreaks of heart rot caused by *Phytophthora*.

Pineapple responds well to the use of organic manures. Growers in 18th-century England allowed sheep to trample their droppings and urine into oak leaves that would be used to make potting compost. More recently, experiments in Hawaii with sewage sludge, chicken manure and dairy or feedlot cattle manure all resulted in substantial yield increases from incorporation of up to about 45 t ha^{-1} (about 20 tons $acre^{-1}$) of manure into lands that had been continuously planted to pineapple for ten to 15 crop cycles. Manures are especially regarded for their high K content. However, virtually all broadcast amendments need to be tested and monitored to ensure that adequate nutrient concentrations are present. To ensure that no surprises occur from the use of manures, representative samples should be analysed both to identify nutrient levels of key elements and to determine pH and soluble salt levels.

Banded preplant fertilizers

The precision placement of preplant fertilizers can ensure both vigorous rooting and the early uptake of N, P and K prior to the development of the leaf canopy. Banded fertilizer should be applied in sufficient amounts to enhance rooting and carry the young plants for 3–4 months, until the canopy is sufficiently developed to make foliar fertilizer applications efficient and effective. Placement is usually just below or adjacent to the plant line to allow the earliest interception by the developing roots. Plastic mulch can protect fertilizer from leaching or volatilization. However, water applied by drip irrigation can contribute to losses by leaching. Many types of fertilizers are available, such as urea, ammonium sulphate, potassium nitrate, superphosphate and treble superphosphate, ammonium phosphate, magnesium sulphate, muriate or sulphate of potash, and others. The choices should complement both the previously incorporated broadcast amendments and, where foliar fertilization is practised, the foliar nutrients that follow later.

Postplant side-dressings and foliar fertilizers

Side-dressings or foliar fertilizers are used where nutrients in the soil are not sufficient to meet the plant's nutrient requirements. Fertilizer may be applied as a dry side-dressing to the soil, often close to the base of the plant or, in some cases, in the lower leaf axils of mature plants. Care must always be taken to avoid plant damage due to exposure to high osmotic concentrations from dissolving nutrients. The basal white tissue of young and expanding leaves is particularly sensitive to fertilizer burn. If manure is to be used as a postplant source of nutrients, infor-

mation on nutrient content, possible microbial contamination and the nature of the composting process may be required.

Foliar fertilizer sprays are particularly effective for pineapple plants and application is easily mechanized (Fig. 6.17A–C). The leaves absorb nutrients through the cuticle and nutrients such as nitrogen, potassium, iron, zinc and boron are readily translocated throughout the plant. The morphological structure of the pineapple plant also facilitates receiving foliar sprays and funnelling them to the adventitious roots at the bases of the leaves, while any overflow is channelled to the dense root mat at the base of the plant. Spray volumes used range from about 225 to 2250 l ha^{-1} (25–250 gallons $acre^{-1}$). The spray volume applied depends on the age of the crop (size of the canopy), the volume of spray required to cover the plant without injuring the basal white leaf tissue and the chemistry of the soluble fertilizers. Although opinions vary regarding the latest age for effective side-dressings or foliar applications, the usual goal is to meet the entire nutrient requirement prior to natural differentiation or forcing.

Ratoons can be fertilized beginning almost immediately after plant-crop harvest. However, because research on the benefits of ratoon-crop fertilization have been largely inconclusive, ratoon fertilizer programmes are inductively designed according to the local conditions, often with about half the foliar fertilizer used for the plant crop.

Diagnostic monitoring of plant health and nutrient status

The crop log, which involved an assessment of plant growth combined with tissue analysis, was a major component of managing plant nutrition on major pineapple plantations. This information, described in more detail by Malézieux and Bartholomew (Chapter 7, this volume) can still be of value in managing the finer details of plant

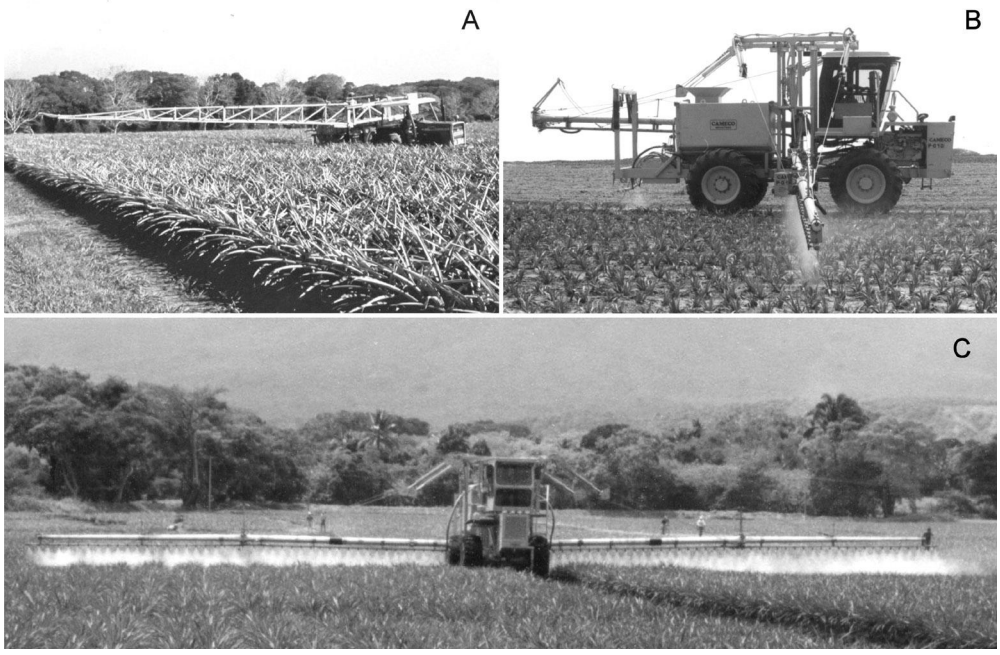

Fig. 6.17. A, Tractor-mounted sprayer with tank trailer on a farm in South Africa (photo courtesy Graham Petty); B, self-propelled boom sprayer with rear-mounted tank (photo courtesy CAMECO Corp.); C, self-propelled sprayer with double boom (photo courtesy CAMECO Corp.).

nutrition. Today, fertilizer schedules for most large operations take into account both research results and operating experiences in order to consistently produce high yields. Such schedules should not be changed unless data gathered at key times during the cropping cycle indicate either a shortfall in or an imbalance of plant nutrients.

Plant nutrient sources and method of application by element

Nitrogen (N)

Broadcast applications of organic compost or manure may preclude the need for additional preplant N, but usually not for postplant N. Where preplant responses are certain, N can be banded in the soil as ammonium sulphate, ammonium phosphate, potassium nitrate, urea or urea-ammonium nitrate at 25–100 kg ha^{-1} (25–100 lb $acre^{-1}$) of N as the element. Side-dressings of ammonium sulphate and potassium nitrate are effective, but prohibitively expensive in large operations. Repeated foliar applications of solutions of urea or urea-ammonium nitrate, at 2-, 3- or 4-week intervals, are the mainstay of the nitrogen programme for most large operations. Cumulative quantities of 200–600 kg ha^{-1} (200–600 lb $acre^{-1}$) of N are typical, depending on the local requirements.

Extensive research has been conducted on the effects of various nitrogen sources and methods of application on the distribution of nitrogen in the plant and the subsequent effect on growth and fruit production (Sideris *et al*., 1934, 1936, 1938, 1947; Sideris and Krauss, 1937; Sideris and Young, 1946, 1947; Su, 1957; Py, 1962; Subramanian *et al*., 1974, 1977, 1978; Chadha *et al*., 1975, 1976; Py *et al*., 1987). For a more detailed discussion of nitrogen and other nutrients, see Malézieux and Bartholomew, Chapter 7, this volume.

An important aspect of nitrogen management is the potential conversion of soil-applied nitrogen to nitrates and the accumulation of these nitrates in the fruit during the later stages of development through early fruit ripening. Application of ammoniacal nitrogen or urea to the leaves almost completely avoids this problem. High nitrates in the fruit are particularly important in fruit canning, where the nitrates rapidly react with the tin coating of the cans, leading to high levels of dissolved tin and development of hydrogen gas, which produces swollen cans (see Hepton and Hodgson, Chapter 11, this volume).

Potassium (K)

Broadcast applications of manure, sulpomag (the natural mineral langbenite containing 22% sulphur, 22% potassium and 11% magnesium), potassium chloride (muriate of potash, KCl) or potassium sulphate (K_2SO_4) are effective at quantities ranging from 200 to 1000 kg ha^{-1} (200 to 1000 lb $acre^{-1}$) of K where soil K is found to be limiting. Potassium can also be banded as sulpomag or as potassium chloride, nitrate (KNO_3) or sulphate at 100–500 kg ha^{-1} (100–500 lb $acre^{-1}$) of K. Side-dressings and foliar applications are also utilized. The requirement for potassium is high, as the plant and fruit remove significant quantities of this element. Plant tissue analysis should show at least 0.20% K on a fresh-weight basis at forcing and responses have been obtained at even higher levels. In sandy soils, potassium should be applied throughout the growing cycle to ensure adequate levels at the time of forcing.

Significant controversy surrounds the form in which potassium should be applied to pineapples, mostly the result of research in Hawaii, where potassium sulphate was shown to be superior to potassium chloride. Organic preplant sources work very well under almost all conditions, but frequently organic sources are not available in sufficient supply. Potassium chloride is almost always the least expensive potassium fertilizer, while potassium nitrate and potassium sulphate are more expensive but provide other nutrients.

Some research has shown fruit quality improvements with the use of potassium sulphate, but this response is by no means universal, and considerable areas of pineapple are fertilized with foliar applications of KCl with no apparent adverse effects on either

yield or fruit quality. To resolve this issue in any particular growing area, comparative trials should be established at various times of the year. Data should be gathered on plant growth, K levels in tissue, and fruit quality attributes to determine if the additional costs associated with K_2SO_4 are justified.

Phosphorus (P)

Phosphorus is most notable for its early enhancement of rooting and yet small effect on final fruit yield. Preplant applications of 25–150 kg ha^{-1} (25–150 lb $acre^{-1}$) of P are often made because of the importance of this element in the development of a strong root system. Phosphorus may be adequate in some soils, but soil analysis may not always reveal the true availability to the plant. Where soil P levels are very low, mycorrhiza may also play an important role in the transfer of this nutrient from the soil to the pineapple plant (Aziz *et al*., 1990). However, soil applications always require an actively growing root system in good health, with adequate moisture supply, for nutrient supply and uptake. In acidic soils, in which pineapple are often grown, finely ground rock-phosphate may be an effective method of supplying phosphorus.

Responses have been obtained to foliar applications of ammonium phosphate, monoammonium phosphate or ammonium polyphosphate. These responses indicate an inadequate uptake of phosphorus by the root system even in areas where standard methods of soil analysis indicate that levels of phosphorus are adequate.

Calcium (Ca)

Lime, gypsum and manure are excellent sources of Ca and typically 200–2000 kg ha^{-1} (200–2000 lb $acre^{-1}$) Ca are broadcast over the field. However, amounts should be determined based on the desired pH and Ca status of the soil. Recommendations for broadcast calcium are complex for pineapple and should be made in conjunction with a reliable soil-testing laboratory and a qualified agronomist. Foliar applications of calcium nitrate or calcium chloride are also possible, but are rarely made and usually pertain to applications after differentiation to enhance fruit quality.

Calcium has been called white gold in reference to the favourable results associated with its use in pineapple nutrition. Dramatic improvements in both fruit yield and quality have been obtained as a result of application following the steady, long-term reduction of soil calcium from the continuous cropping of pineapples. The method of calcium application and incorporation must be well understood if favourable results are to be consistently obtained and potential disasters associated with high soil pH and increased incidence of *Phyphthora* root and heart rots are to be avoided. The judicious use of calcium to increase its content in soil and raise soil pH results in enhanced uptake of other nutrients. At the same time, the additional calcium produces stronger cell walls, which result in better plant growth and development of fruit that are more resistant to bacterial diseases (see Rohrbach and Johnson, Chapter 9, this volume).

Iron (Fe)

Repeated foliar applications of ferrous sulphate (1% solution) in the same foliar solution with N are very effective. Leaf deficiency symptoms for iron are distinctive for pineapple and are an excellent guide to the need for iron. Where iron deficiency is certain, foliar-applied Fe will increase the yield of pineapple in proportion to the amount required to remove an observed Fe deficiency. Application rates can be determined for the current crop and empirically for subsequent crops based on visual monitoring of leaves. Cumulative amounts from repeated foliar sprays may vary from 2–10 kg ha^{-1} (2–10 lb $acre^{-1}$) of Fe in the plant crop and 1 to 5 kg ha^{-1} (1–5 lb $acre^{-1}$) of Fe in the ratoon.

To avoid precipitation, ferrous sulphate should not be used in a foliar solution with phosphate or boron. Care must also be taken to avoid foliar burning due to the high osmotic potential of ferrous sulphate. In the case of low-volume applications, there should be no runoff into the leaf axils where

the sensitive basal white tissues are located. The quality of the ferrous sulphate, which is green in colour, needs to be confirmed, since the iron is readily converted in moist air to the ineffective ferric form. Chelated sources of iron are effective, but can be prohibitively expensive and may deteriorate in storage. Soil or drip application of iron, even in chelated form, is costly or not consistently effective, or both.

Magnesium (Mg), zinc (Zn), boron (B) and other micronutrients

Deficiencies of Mg, Zn and B may occur, but are not commonly encountered. Broadcast magnesite, dolomite or sulpomag (also called K-Mag) at 100–500 kg ha^{-1} (100–500 lb $acre^{-1}$) of Mg provide an excellent long-term correction for soils deficient in Mg. For the immediate correction of Mg deficiency in pineapple, a series of foliar applications of magnesium sulphate (Epsom salts) are applied in combination with other sulphates, such as Fe or Zn. Cumulative amounts from repeated foliar sprays may range from 10 to 50 kg ha^{-1} (10–50 lb $acre^{-1}$) of Mg in the plant crop and 5 to 25 kg ha^{-1} (5–25 lb $acre^{-1}$) of Mg in the ratoon.

Since a deficiency of Zn or B can be especially devastating, they are applied when even marginally low levels are suspected. Zinc and boron are truly microelements and should not be overapplied. Zinc sulphate is applied in combination with other sulphates, such as Fe or Mg, to achieve a total application of no more than 0.1 kg ha^{-1} (0.1 lb $acre^{-1}$) of Zn. Boron should not be applied in combination with any other nutrient; it should be applied at about 1.0 kg ha^{-1} (1.0 lb $acre^{-1}$) of B in one or two foliar applications. Soluble forms of borax are available from qualified fertilizer dealers. In Queensland, Australia, boron is commonly applied in the ethephon solution at 10 kg $acre^{-1}$ of borax or solubor, when plants are forced, to supply B and, especially when forcing in midsummer (January–February), to raise the pH of the ethephon solution to enhance forcing success. Under these conditions, boron is applied in a 2.0–4.0% urea solution.

Deficiencies of copper and molybdenum are also sometimes encountered (see Malézieux and Bartholomew, Chapter 7, this volume). Care should be exercised when applying these micronutrients because their use in areas not showing deficiency could result in foliar damage due to toxicity.

Flower Initiation and Fruit Development

Natural differentiation

The physiology of flowering in pineapple is covered elsewhere (see Bartholomew *et al.*, Chapter 8, this volume). However, certain aspects of the implications and occurrence of natural differentiation are discussed below. Pineapples flower naturally under certain conditions and these conditions vary somewhat in different parts of the world. However, natural flowering may be generally classified as winter or short-day-length-, cold-weather-induced flowering, and summer or dry-weather-induced flowering. Other stress factors, such as root damage from pathogens or waterlogged soils, may also induce flowering.

The above factors usually result in a slowing of vegetative growth, with a corresponding increase in starch accumulation in the leaves and stem. Critical levels of starch accumulation have not been determined, but there have been clear demonstrations that the summer flower-initiation period can be minimized or avoided by ensuring adequate supplies of nitrogen and water to promote active vegetative growth.

The effect of low temperatures and short photoperiods during winter on natural flowering can be reduced in plants by maintaining high plant nitrogen status, but nitrogen alone cannot eliminate differentiation if air temperature drops below 15°C (60°F).

Chemically induced flowering

In the early 1700s, fumes from fires used to heat pineapple houses were observed to force the induction of flowering and this finding led to the commercial use of smoke

for this purpose. The active ingredient in smoke was shown to be ethylene (Rodriquez, 1932) and later work (Kerns, 1936) showed that acetylene also forced flower induction. This finding prompted the use of carbide as a source of acetylene, a method still widely used on small farms. A pea-sized amount of calcium carbide is dropped into the centre of the rosette of leaves of a vegetative plant of sufficient size. The carbide reacts with water to release acetylene, which is taken up by the leaves. Acetylene (Aldrich and Nakasone, 1975) and ethylene, which much research shows is the most effective forcing agent (Bartholomew and Criley, 1983), are both more effective if applied at night when the stomata are open.

Synthetic auxins such as α-naphthalene acetic acid (NAA) initiate flowering of pineapples by promoting the synthesis of ethylene by the plant (Burg and Burg, 1966). These materials significantly reduced the cost of forcing, while maintaining a high degree of forcing efficiency. The most widely used synthetic auxin was the sodium salt of naphthalene acetic acid (SNA). As little as 50 g ha^{-1} in 2800 l of water (20 g $acre^{-1}$ in 300 gallons of water) could initiate flowering. Usually, two applications, a week apart, were made. This ensured that any plants not initiated by the first application were induced by the second.

The newest material used as a forcing agent is ethephon (2-chloroethylphosphonic acid). Ethephon is typically applied in combination with urea and, in some areas, sodium borate or calcium or sodium carbonate (Dass *et al.*, 1976; Balakrishnan *et al.*, 1978). The latter materials raise the solution pH, which hastens the rate of breakdown of ethephon into ethylene. For more details, see Bartholomew *et al.* (Chapter 8, this volume).

A variety of combinations of the above materials have been evaluated for commercial forcing. Best results go beyond just the percentages of plants that are forced and should include the uniformity of the harvest peak and the fruit yield. In this regard, commercial forcing with ethylene has shown outstanding results. However, this practice requires that 3000–4000 g ha^{-1} of ethylene gas be adsorbed on to activated carbon or a fine clay, such as bentonite. Typically, the ethylene and 22 kg of adsorbent are applied in 4500–7000 l ha^{-1} of water at night when the stomata are open. The large quantities of water required and the need for specialized equipment have generally limited this practice to the largest growing operations, although smaller farms in Côte d'Ivoire also force with ethylene. More generally, ethephon is used for knapsack and small and large boom applications, and the quantities being used vary with area and season and are limited by label requirements.

To determine the efficacy of the forcing operation, representative plants may be cut longitudinally through the apex, to observe the development of the young inflorescence. This is done at 6–8 weeks after forcing and may be repeated at weekly intervals until 95% or more of the plants have differentiated. Areas that do not attain 95% can be reforced.

Plant weight–fruit weight relationships

To provide an adequate-size fruit for fresh market or for canning, plants are grown to a prerequisite weight before forcing. The ideal plant weight depends on a variety of factors, the more important ones being temperature, solar radiation, water and planting density. Plant nutrition is important, but the effects of nutrition are also seen in the time taken to obtain the prerequisite plant weight and the rate of growth at the time of forcing.

When plants were grown under conditions that provided an identical rooting environment and nutrition, with only the climatic factors varying, a clear relationship existed between dry matter accumulated in the plant stem, expressed as a fraction of total plant dry matter, and the subsequent fruit weight (Hepton *et al.*, 1993). Dry-matter accumulation appears to fall within predictable ranges in various growing areas, with additional seasonal variation occurring as these areas become farther removed from the equator. Differences in dry matter accumulation are due to differences in day length and day-to-night temperature variations. Consequently, relatively small plants (less

than 2 kg fresh weight) can produce fruit weighing more than 2 kg at certain times of the year in Hawaii, resulting in a fruit-to-plant ratio of more than 1.0. In comparison the ratio in the Philippines is about 0.65 and in Thailand about 0.46. These ratios can change if practices result in plants with a higher percentage of dry matter at the time of forcing. As was noted previously, average fruit weight declines as planting density increases (Fig. 6.10).

Other Cultural Practices

Slip removal

Some varieties and some clones of 'Smooth Cayenne' have a large number of slips. Though useful as planting material, if left on the plant through fruit development, they can severely reduce fruit yield. Slip numbers tend to be a function, first, of variety or clone and, secondly, of environmental and forcing conditions. Plants forced with SNA tend to have fewer slips than those forced with ethylene. This difference is attributed to the ability of ethylene to promote floral differentiation of lateral buds as well as the apical meristem. Each lateral bud, once differentiated, becomes a miniature fruit with a crown, i.e. a slip. To minimize the adverse effects of slips on fruit yield, they should be removed as soon as this can be accomplished without damaging the peduncle of the developing fruit.

Sucker pruning

The development of suckers appears to be a function of variety and plant vigour. Some varieties, e.g. 'Queen', produce numerous suckers, which arise from leaf axils at or above ground level. High numbers of suckers make ratooning very difficult, because ideally the plant should have one high-quality sucker to replace the mother plant, thereby retaining the original planting density.

'Smooth Cayenne' sucker numbers are influenced by planting density, plant weight at the time of forcing and nutritional status. Environmental factors that result in high carbohydrate accumulation in the stem of the plant–crop plant will increase the number of sucker buds that develop.

Large plants in a population will tend to develop one or more suckers early during fruit development, while sucker development on smaller plants may be significantly delayed. To provide uniformity in the ratoon crop, large suckers may be removed, a standard practice in some fields in Thailand. Additional suckers will develop from the axillary buds that are already present. Sucker pruning improves the uniformity of ratoon crops, but it will increase the time required to reach the predetermined average sucker weight at forcing. Pruning of suckers will also reduce yield per area per unit of time. Consequently, the decision to prune or not to prune suckers will depend on the purpose for which the crop is being grown, the projected harvest date and, in some areas, the potential for using the pruned suckers as a source of planting material.

Because sucker pruning is labour-intensive, it is generally practised in growing areas where the cost of removal is offset by the increased value of the larger and more uniform ratoon fruits and the value of suckers as planting material. The value of an earlier harvest from fields planted with suckers must also be taken into consideration.

Crown gouging

When fruit develop under conditions that favour vegetative growth, there is often a significant growth spurt to the crown in the final weeks of fruit development. If the apical growing point of the crown is removed or damaged before this growth spurt occurs – usually 10–12 weeks before harvest – an increase in fruit weight of 6–10% can be obtained.

Crown gouging is not an option in areas where crowns are a primary source of planting material. Crowns are one of the least expensive forms of planting material. With modern equipment, crowns can be detached from the fruit, dipped in pesticides to control

disease and insects and conveyed to separate bins for transport to areas where they will be planted. In some systems, crowns are separated from the fruit during harvest and transported to the processing factory, where they are separated from the fruit by forced air.

Crowns should also not be gouged in fields where high nitrates in the fruit could be a problem. The continued growth of the crown ensures movement of nitrates through the fruit to the expanding crown leaves. If this process is stopped by gouging, nitrates will accumulate in the upper portion of the fruit. As noted previously, high fruit nitrate levels are problematic in processing, and the situation is further aggravated if the fruit is not fully ripened at harvest.

Crown removal

As with crown gouging, crowns may be removed to promote fruit expansion. In multicrowned fruit, removal of all but one crown with a sharp knife or scalpel will improve fresh-fruit marketability. When a crown or crowns are to be removed, the practice should occur earlier than for crown gouging and crowns should be sufficiently well developed to allow for easy removal without damage to the fruit. Crown removal is labour-intensive and may not be practical in all areas, but, when it is performed by practised workers, the scar tissue is barely visible when the remaining crown is fully developed. If the crown has grown large enough to shade the shoulders of the fruit, it may be better to retain the crown to prevent fruit sunburn. This problem is serious in areas of intense sunlight.

Leaf pruning

In some growing areas, leaves are pruned to facilitate entry into the field for various activities, particularly harvesting. All evaluations of leaf pruning have shown that yields are reduced proportionate to the amount of leaf removed (Pineapple Research Institute of Hawaii (PRI) data), and the earlier the removal takes place, the greater the impact (Fig. 6.18). Leaf removal also has an adverse effect on the growth of both slips and suckers (Fig. 6.18). The reason for this dramatic impact is twofold: first and most obvious is the reduction in the supply of metabolites from the leaf canopy; and second is the loss of dry matter already accumulated in the leaves, which would be available for fruit

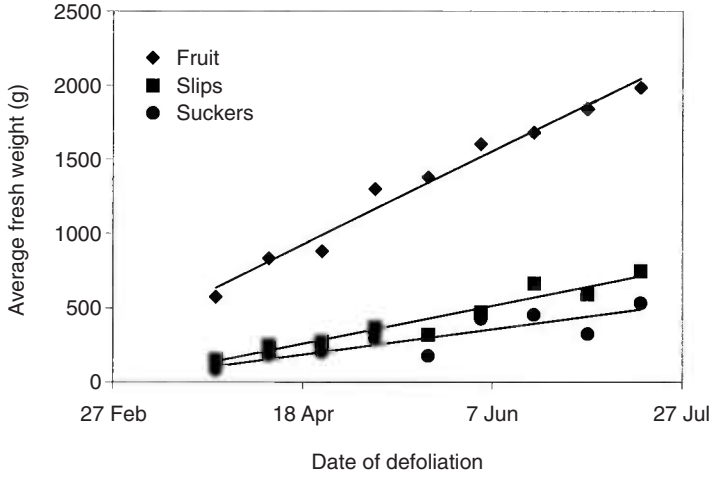

Fig. 6.18. Effect of date of leaf defoliation on average fresh weight of fruit ($y = 635.4 + 12.57x$, $R^2 = 0.98$), slips ($y = 141.17 + 5.11x$, $R^2 = 0.92$), and suckers ($y = 106.5 + 3.42x$, $R^2 = 0.76$) of 'Smooth Cayenne' pineapple in Hawaii; $n = 9$ for all (A. Hepton, unpublished results).

development (King, 1935). Carbohydrate allocation and reallocation during fruit development are discussed in Bartholomew *et al*. (Chapter 8, this volume).

Preharvest Fruit Treatments

Postforce and preharvest nutrition

Generally, yields from plants that have adequate nutrition during vegetative growth do not respond to additional nutrition during fruit development. However, applications of nitrogen during the later stages of fruit development may increase vegetative growth of developing suckers. This can be important when good sucker growth is required, where suckers are to be harvested for planting material or to optimize ratoon yields. When other nutrients such as boron, iron or calcium, are deficient, their addition may increase fruit yield or quality, or both.

Protection against sunburn

In areas with high irradiance during the later stages of development, sunburned fruit can be a serious problem. Temperatures on the fruit surface can exceed 55°C (130°F), leading to cell death, tissue collapse and dehydration. In some cases, the tissues may be attacked by insects or disease organisms.

To minimize or avoid this problem, a number of solutions have been devised. The techniques all seek to reduce direct radiation of the fruit surface. Popular methods include tying of the longest leaves above the fruit, covering susceptible areas with rice straw or other convenient dry vegetation, the use of shade cloth or the use of newspaper or other paper caps positioned to cover the shoulders of the fruit. When shade cloth is used, it could have an adverse effect on fruit yield if it covers the entire plant. Reflective sprays containing calcium carbonate and a sticker have also been used to coat susceptible areas of the fruit. A number of commercial mixtures are available that can be washed off the fruit after harvest.

Where sunburn is a problem, early gouging of crowns should be avoided in order to retain the benefit of this source of natural shade. The more serious problems of sunburning occur in ratoon fruit during the later stages of development. Sunburn often develops when the heavy fruit causes the sucker to lodge, exposing the previously unexposed broad side of fruit to direct sunlight. Additionally, lodged fruit are below the level of the canopy and so cannot benefit from convective cooling by winds. The problem of sunburn is accentuated on border rows, where the fruit may be larger and there are no adjacent plants to help support the fruit. Some relief to the situation can be obtained by planting the outside line at a higher density relative to the rest of the field so as to reduce the fruit weight.

Ripening acceleration

Ethephon is effective in both accelerating the ripening process and concentrating the harvest peak, allowing complete harvest in fewer passes. Both the timing and quantity of ethephon are important for optimizing these processes. Application too early slows important aspects of the ripening process – in particular, full cellular expansion and the accumulation of sugars and flesh pigments – thus reducing fruit weight and quality. High rates of application, while accelerating the rate of degreening, may also reduce yield and, if large suckers are present, they may be forced by the ripening treatment. This would result in small, early fruit if the suckers were retained for a ratoon crop, or if the suckers were intended for propagation they would be rendered useless.

Irrigation during fruit development

As noted previously, pineapple plants require about 5 cm (2 in.) of water per month. This requirement continues during fruit development, and drastic changes in moisture status should be avoided. Drip irrigation can be continued until just prior to harvest. Overhead irrigation should be avoided after the onset of the open-petal stage of flowering. This will minimize fruit diseases, while having little adverse effect on yield.

Harvesting

Determining the state of maturity

The state of maturity at which fruit are harvested will depend on the variety or clone, the purpose for which the fruit are being harvested and the environmental and growing conditions. Other factors, such as the potential for fruit diseases or high nitrates, expected or recent weather conditions and labour supply, can influence decisions on when the fruit is actually harvested.

Most fruit is harvested by the appearance of the external colour of the shell. The recommended shell colour for harvest is determined by evaluating the relationship between the external appearance and internal characteristics. Often, fruit are sampled at a number of shell colours, and flesh Brix (total soluble solids, %) is measured to determine the degree of flesh maturity at each colour. Minimum Brix levels are required in many markets for fresh fruit. The Revised Codex Standard for Pineapples (CODEX STAN 182–1993 (Rev. 1–1999), FAO/WHO Codex Alimentarius Standards, Vol. 5B, Codex Standards for Tropical Fresh Fruits and Vegetables, Secretariat of the Joint FAO/WHO Food Standards Programme, Food and Agriculture Organization of the United Nations, Viale delle Terme di Caracalla, 00100 Rome, Italy) has set a minimum of 12°Brix for fresh pineapples in international trade.

For fruit destined for both cannery and fresh market, fruit translucence (Fig. 6.19) may also be an important factor in determining the shell colour at harvest. For additional details, see Hepton and Hodgson (Chapter 11, this volume).

Hand-harvesting

Most of the world's pineapples are harvested by hand. For cannery processing, fruit are picked and placed into bags or baskets for

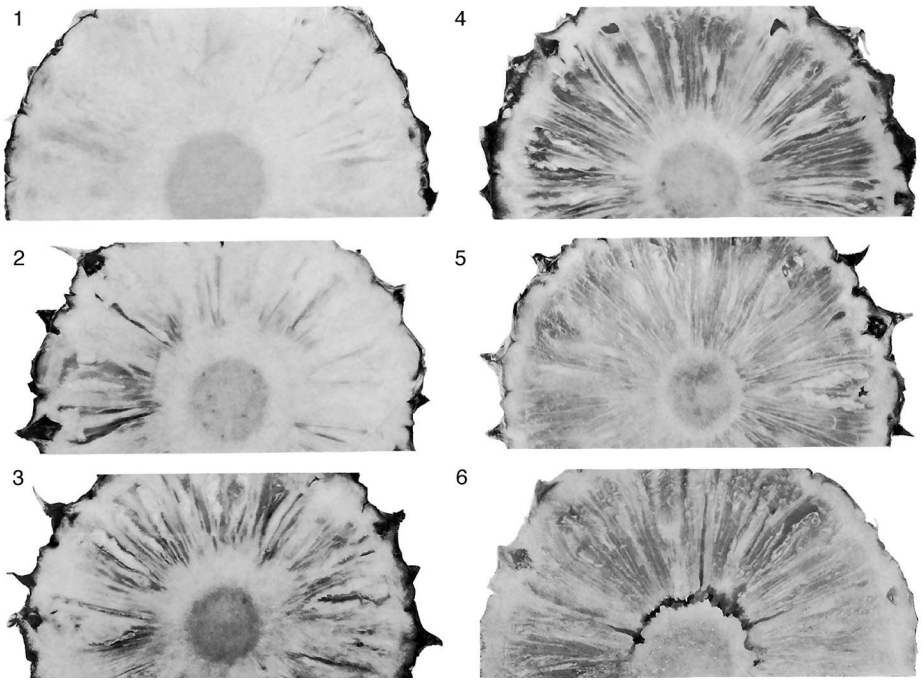

Fig. 6.19. Slices of 'Smooth Cayenne' pineapple fruit showing the range from opaque (not translucent) to fully translucent (photo courtesy of W.G. Sanford).

removal from the field. The fruit may be accumulated at roadways for transfer into trucks (Fig. 6.20) or loaded directly for transportation to either the cannery or a central location, such as a broker, where fruit can be accumulated before transfer to the cannery. Harvested fruit should not be left exposed to direct sunlight for more than an hour or so, as the sides and lower parts of the fruit are susceptible to sunburn.

Fruits destined for fresh market are usually harvested with the crowns and are often cut from the plant with a short length of peduncle remaining attached to the fruit. For local markets, the peduncle length may be 5–10 cm long, but for international trade, peduncle length is limited to 2.0 cm under the Codex standard referred to above. On some farms and plantations, fresh fruit are packed directly into shipping boxes in the field. Cut surfaces on these fruit may be treated with fungicides to reduce black rot and waxed to help retain fruit quality.

Machine-assisted harvesting

A wide diversity of machines have been developed to assist in the harvesting of pineapples. Truck-mounted or 'parasitic' systems are mounted on the bin that will receive the fruit and are moved by the truck carrying the bin (Fig. 6.21). Others are tractor-drawn or self-propelled and move at the same speed as the bin mounted either on a truck or trailer pulled by a tractor (Fig. 6.22). Basically, all harvesters are a series of conveyor belts that assist by moving the fruit from the pickers to the transportation bin.

Cannery fruit may have the crowns removed and the crowns may be left in the field or conveyed in the transportation bin to cushion the fruit against bruising. Later, the crowns may be separated from the fruit at the cannery and used as planting material. Some machines have been developed for fresh-fruit harvesting and in-field packing. These machines are large and heavy and are designed to be operated in relatively flat areas under dry conditions.

Transportation of Harvested Fruit

Movement of pineapple from the field to its ultimate destination requires an understanding of the physiology of the fruit after harvest. If the travel time is short, as in the case

Fig. 6.20. Hand-harvested pineapples being loaded on a truck for transport to the processing plant in Johor Baru, Malaysia.

Fig. 6.21. Bin-mounted 'parasitic' harvester that moves with the truck while fruit are being picked.

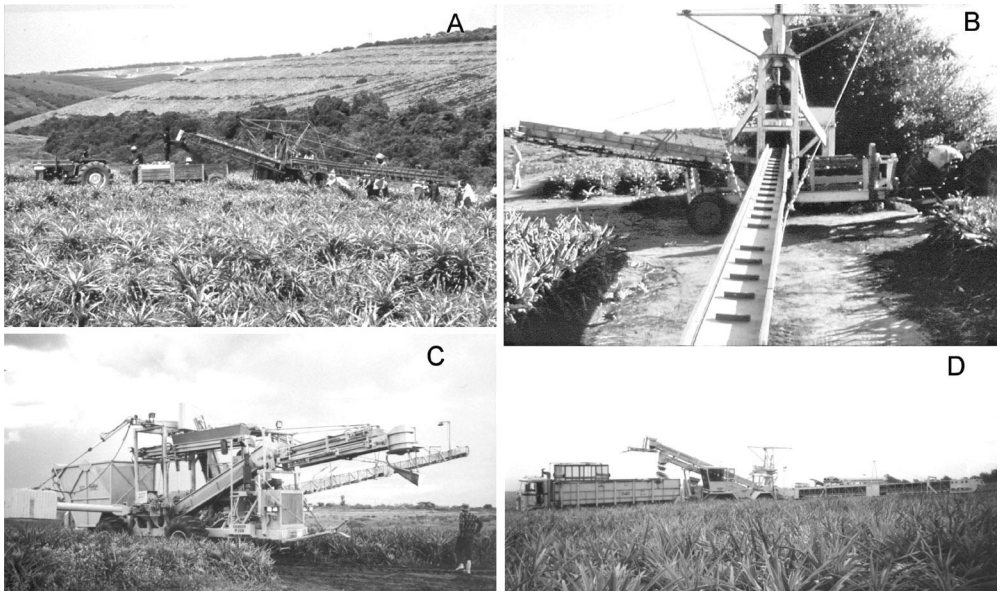

Fig. 6.22. A, Tractor-drawn harvesting equipment used in the field in South Africa and B, close-up of harvester (photos A and B courtesy of Graham Petty); C, self-propelled harvester with bin for temporary storage of crowns to be used for planting material; D, self-propelled harvester following truck with movable bed to facilitate unloading of fruit at the cannery (photos C and D courtesy of CAMECO Corp.).

where the fields are near the cannery, the key aspects are to move the volume of fruit efficiently, while minimizing damage. Damage, which reduces slice recovery, can occur from bruising during loading, transportation, unloading and conveying in the cannery system.

To understand the sources of bruising, extensive studies were conducted, evaluating the depth of loading in bins, the types of

suspension on trucks, road conditions and the movement of fruit that result in impacts with stationary surfaces or with other fruit. As a result of some of these studies, some fruit are now transported with crowns, while other fruit are carefully stacked end to end in layers to minimize damage.

Fruit being transported to fresh markets fall into two major categories. Some are destined for the local market, while others are shipped significant distances by air, sea or long surface hauls. If the transportation, including air transportation, takes only 1–2 days, the fruits may not require refrigeration. However, fruit quality is usually improved if the fruit is picked ripe and held under refrigeration. Fruit that will be transported for 3 or more days should be refrigerated at temperatures between 7.2 and 10°C (45 and 50°F). Additional details of postharvesting handling of fresh fruit can be found in Paull and Chen (Chapter 10, this volume).

Ratooning

The practice of harvesting a second or additional crops from an original planting is known as ratooning. Ratoon crops are important in pineapple crop management, where they reduce costs when they can be harvested more economically than replanting the same or another area. They also provide a range of fruit sizes that complement the plant crop in the cannery and provide crowns for planting material. Generally, they provide high-quality fruit at a lower cost than plant-crop fruit and in a relatively shorter time.

In some growing areas, replanting may be done infrequently, if at all, and all fruit are harvested from ground suckers that grow from the previous crop. This practice was once common on the peat soils in Malaysia, which cannot support heavy tillage equipment. On these soils, replanting was limited to replacement of missing plants. A disadvantage of this system is the loss of uniformity and synchronization of the crop in successive years. Suckers were forced individually when they reached an adequate size, and fruit was harvested through most of the year in all fields. At present, at least one of the larger growers in Malaysia grows only a plant crop on peat soil. After harvest, the foliage is desiccated with a herbicide and burned and the field is replanted with suckers.

The more conventional first and second ratoon crops, grown in areas where sucker growth is fair to good, allows most of the suckers to be forced together. When practices such as sucker pruning have been used, there is an improvement in crop uniformity. Ratoon crops are fertilized, irrigated, forced, ripened and harvested in much the same way as the plant crop, though the amount of fertilizer applied is usually reduced. Practices such as ripening with ethephon may actually be easier if the ratoon fruit being treated is the last before knockdown and the following suckers will not be used as planting material for another crop.

Successful ratoon production is dependent on a healthy root system. This requirement presents a challenge in areas infested with root-knot or reniform nematodes. Other potential root problems, such as grubs, symphylids and root-rotting fungi, can limit ratoon production; these are covered in Rohrbach and Johnson (Chapter 9, this volume).

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7 Plant Nutrition

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Plant Nutritional Status

The nutritional status of the pineapple plant has a large influence on plant growth and, consequently, on yield and fruit quality. For pineapple, plant indicators that reflect plant nutritional status have been identified and, in conjunction with soil analysis, can be used to manage fertilization of the pineapple crop. The alternative to the use of plant indicators and soil analysis is the use of calibrated fertilizer trials in each area where the crop is grown. This practice is more common where pineapple is grown on small farms and where access to technology is limited (Souza, 1999). To sustain growth and obtain good yields, it is important to provide adequate supplies of all nutrients in proper balance. Balanced nutrition based on the principles of best management practices ensures that excess nutrients of one type do not induce deficiencies of others or, in the case of N and P, lead to environmental degradation.

The plant indicators of nutritional status include visual deficiency symptoms and the critical nutrient levels in appropriate reference-plant tissues. This tissue in pineapple is the 'D' leaf, which in most cases is the tallest leaf on the plant. The D-leaf is used because it is the only leaf that can be consistently identified and, as the youngest almost physiologically mature leaf, it reflects current plant nutrient status with acceptable accuracy. Sideris and Krauss (1936) categorized (Fig. 7.1) leaves as: 'A', present on the propagule at planting and do not elongate after planting; 'B', present on the propagule at planting and elongate after planting; 'C', leaves that develop after planting and are younger than 'B' leaves but older than 'D' leaves; 'D', a whorl of three leaves, including the tallest on the plant; 'E', a whorl of three leaves younger than the 'D' leaves; and 'F', a whorl of three leaves younger than the 'E' leaves. As the plant grows, leaf classification continuously changes, so that 'F' leaves become 'E' leaves, 'E' leaves become 'D' leaves, and so on. A knowledge of the visual symptoms associated with the deficiency of a specific nutrient can help with early detection of nutritional problems in the field. Nutrient levels in leaf tissue provide information about the quantity of nutrients actually absorbed by the plant. However, nutrient deficiencies can have multiple origins, which need precise identification, and several nutrient-deficiency symptoms are not diagnostic.

A diagnosis reference system

The nutritional status of a pineapple plant depends on many factors, including the nutritional status of the propagule, soil

 The Pineapple: Botany, Production and Uses (eds D.P. Bartholomew, R.E. Paull and K.G. Rohrbach)

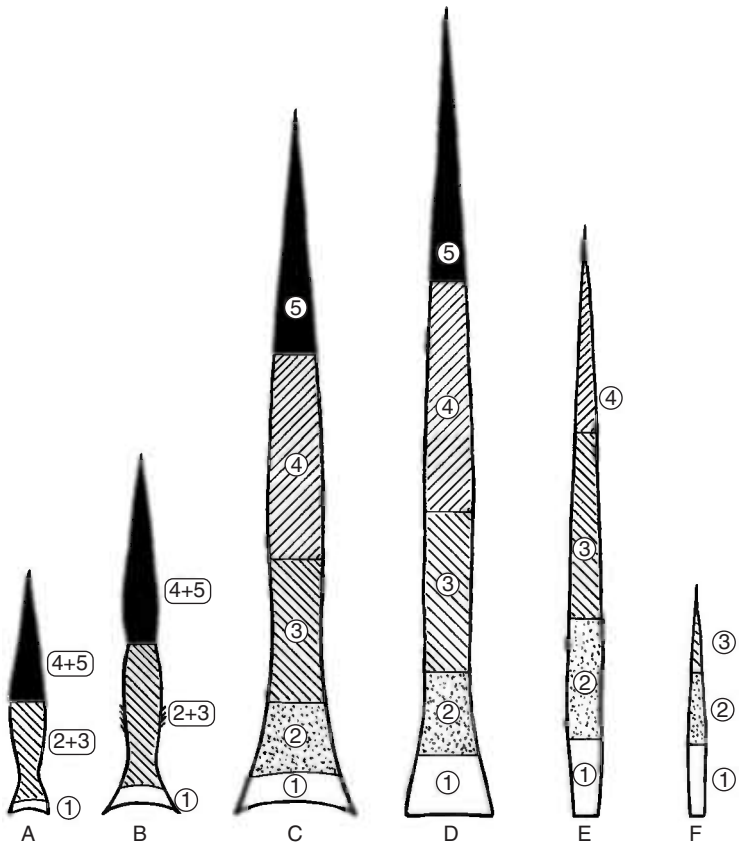

Fig. 7.1. Groupings of pineapple leaves after Sideris and Krauss (1936). The numbered sections of each leaf refer to the following tissues: 1, basal non-chlorophyllous; 2, transitional subchlorophyllous; 3, lower chlorophyllous; 4, intermediate chlorophyllous; 5, terminal chlorophyllous. (Drawing modified from Sideris and Krauss, 1936.)

nutrient status, the physical and mineral characteristics of the soil, soil water status, root-system development and functionality and numerous physical and biological factors that can influence the efficiency of the root system in extracting soil nutrients. Pineapple readily absorbs all nutrient elements through the leaves (Py *et al.*, 1987), but N, P, K, Mg, Fe, Cu, Zn and B are the ones most commonly applied in solution foliarly (Swete Kelly, 1993). Calcium is normally not applied foliarly because most salts of Ca are relatively insoluble or would render other nutrients in a solution insoluble. Also, calcium is relatively immobile in plants, so foliarly applied calcium may not move to tissues where it is deficient. Where foliar absorption replaces soil uptake, nutrient utilization is still dependent on the physical and biological factors that affect the extraction and utilization of plant nutrients in the soil.

The concept of a pineapple crop log was established in Hawaii in the 1940s (Sanford, 1962), and comprehensive knowledge of nutrient management was developed in many countries in the 1960s and 1970s. The crop log includes soil and plant indices as well as those biological and physical factors of the pineapple crop environment likely to influence growth (Sanford, 1962). The consistent use of the crop log during plant development allows for the detection of factors

likely to retard growth and provide growers with the information required to adjust fertilizer applications to fit the requirements of the crop. However, no integrated diagnosis database capable of synthesizing this information is available.

The crop log, as embodied in the work of Nightingale (1942a,b) and more completely characterized by Sanford (1962), includes indices related to the actual determination of nutrient deficiencies and those that measure other factors that may have a direct or indirect effect on the nutrition of pineapple plants. The first set of indices include soil analysis, plant visual deficiency symptoms and plant analyses. The second set of indices include growth rates, plant pests, moisture status and weather. Thus the crop log not only identifies those nutrients that are limiting, but also provides information on why they are low. For example, the presence of a nematode or fungus infestation of roots or inadequate soil moisture could explain why a nutrient element is deficient in a plant even when levels of a given element in the soil are satisfactory.

To ensure that growth is optimum, it is essential to identify all the factors that directly or indirectly affect the uptake, translocation and utilization of nutrients. Soil indices always include the levels of P, K, Ca and Mg and pH, but may also include soluble Al and Mn and salinity. Where nitrate in fruits is a concern, soil N may also be analysed (Swete Kelly, 1993). When properly developed and calibrated, soil analyses provide an estimate of the quantity of fertilizer to be applied at planting and during early growth, indicate the levels of nutrient element reserves in the soil and indicate possible toxicities that could restrict plant growth.

Opinions about soil nitrogen analyses vary. In Hawaii, soil N analysis was not considered to be useful because the results were too variable (Sanford, 1962). Also, pineapple plants had a low requirement for N during early growth, so the relationship between soil N and early growth was poor. However, in Australia (Sinclair, 1993), both initial soil N as nitrate and nitrate present after a 2-week incubation period are provided for growers to guide them in applying nitrogen fertilizer prior to planting. Since growers often tend to over- rather than underfertilize, soil N analyses help to reduce the problem of high nitrate in fruit at harvest (Sinclair, 1993).

Plant indices for N, P, K, Ca, Mg and Fe have been developed using the 'D' leaf, but may include other elements as well (Table 7.1). If measured, N and Fe are analysed on the middle one-third of the green tissue of this same leaf. However, plant N status is assessed visually in Hawaii and Australia, using plant colour, as described by Nightingale (1942a), because N levels in

Table 7.1. Norms proposed for 'D'-leaf mineral element content.

	Basal white*†			
Element	Vegetative	Induction	Deficient	Whole leaf‡ inflorescence emergence
N				15–17 g kg^{-1}
P	110	200	<100	~1.0 g kg^{-1}
K	3000–3500	3000	2000	22–30 g kg^{-1}
Ca	150	150	90	8–12 g kg^{-1}
Mg	250–270	250–270	90	~3.0 g kg^{-1}
Zn				10 mg kg^{-1}
Cu				8 mg kg^{-1}
Mn				50–200 mg kg^{-1}
Fe				100–200 mg kg^{-1}
B				30 mg kg^{-1}

*Units are in mg kg^{-1}, fresh-mass basis.
†Data from Glennie, 1977; Swete Kelly, 1993.
‡Data from Dalldorf and Langenegger, 1978.

pineapple leaves can change quickly and so were not found to be a reliable measure of long-term plant nitrogen status.

Tissue element norms for P, K, Ca and Mg for 'Smooth Cayenne' were developed for the middle one-third of the white basal tissue of the 'D' leaf in Hawaii and Australia, because the results can be expressed on a fresh mass basis, thus simplifying calculation of the final results (Table 7.1). The fresh mass of basal tissue can be used because changes in the dry-matter content of this tissue with changing plant water status are small, typically only 1.0–1.5% (Sanford, 1962). The analyses are usually made on ten 'D' leaves sampled from a crop logging station comprised of about 100 plants in a representative part of the field.

Tissue element norms have also been developed for the entire 'D' leaf (Py *et al.*, 1987; Table 1) because it was believed that nutrient element levels in leaf basal tissue were more indicative of movement within the plant and were too sensitive to daily rhythms and to variations in the soil solution. Because whole-leaf water content can vary significantly, results must be calculated on a dry-mass basis. There is little evidence to show that one method is superior to the other and it is clear from a long history of use that either method allows for the early detection and correction of nutrient-element insufficiencies.

Few data are available on possible differences among cultivars. Optimum levels of N, P and K in 'Red Spanish' pineapple appear to be slightly higher than those for 'Smooth Cayenne' (Samuels and Gandia-Diaz, 1960). While published data were not found for pineapple hybrids, tissue levels of nitrate-N, P, K, Mg and B were higher for the hybrid '53–116' developed by the Pineapple Research Institute of Hawaii than for the 'Smooth Cayenne' clone Champaka F153 at the same level of applied nutrients (Anon., 1965). It should not be assumed that the nutrient requirements of hybrids will be the same as those for 'Smooth Cayenne'.

Distribution of nutrients within the plant

The nutrient content of any tissue depends upon its physiological age. However, because approximately 80% of a typical vegetative pineapple-plant fresh or dry mass is leaves (see Malézieux *et al.*, Chapter 5, this volume), leaves are the focus of most of the discussion that follows. Young, actively growing leaves (leaves younger than the 'D' leaf) generally have higher nutrient levels than do older leaves that are fully grown (Sideris *et al.*, 1943; Sideris and Young, 1945, 1946). The nutrient content of any given leaf increases from the base (youngest tissue) to the tip (older tissue) (Sideris *et al.*, 1943; Sideris and Young, 1945, 1946). Leaf dry-matter contents of the basal portions of 'C' leaves are higher than in younger leaves and the dry-matter content of all leaves increases from the base to the tip, while that of the stem decreases from the base to the tip.

The total amount of nutrients in the plant increases with age but the concentration in any given tissue can increase, decrease or remain unchanged, depending on the nutrient and the tissue. Assuming no other limitations, nutrient concentration in the plant tends to reflect the supply available, whether provided by foliar feeding or by the soil, especially where the supply is limiting. When fertilizer applications are made, 'D'-leaf nutrient concentration may temporarily increase in response to those applications, even though the long-term trend of nutrient concentration in the 'D'-leaf basal tissue is downward with increasing time after planting. Seasonal changes in tissue nutrient concentrations occur (Sanford, 1962), but they may result from changes in the plant growth rate rather than from changes in nutrient availability to the plant. Much of the available data on plant nutrient composition over time were collected before pineapple was planted throughout the year so it is uncertain if changes with season and plant age are due to plant age or to weather-induced changes in growth rate. It would be worthwhile to collect data on leaf-tissue nutrient content from well-grown plants of the same age at different times of the year to further evaluate these plant-age–environment interrelationships.

Visual deficiency symptoms of each nutrient were reproduced for pineapple in the early 1960s by growing plants in single-

nutrient cultures in solution or sand, with all other nutrients but the one being studied kept at optimum levels. These experiments were mainly conducted on 'Smooth Cayenne' (Sideris and Young, 1951, 1956; Cibes and Samuels, 1961; Tisseau and Tisseau, 1963), although 'Singapore Spanish' (Kanapathy, 1959) and 'Red Spanish' (Cibes and Samuels, 1958) were also studied. These visual symptoms and the leaf concentrations of the nutrients associated with them are of use in diagnosing nutritional problems in the field. However, multiple deficiencies may occur in the field, which can make diagnosis difficult without confirming plant-tissue analyses, as well as an analysis of the plant and its soil and aerial environment.

The symptoms described below and their associated 'D'-leaf nutrient concentrations are quite specific and, when they occur, are easily observed in the field. Information about optimum levels of the nutrient in soil are also provided. They were reported previously (Py *et al.*, 1987; Swete Kelly, 1993) or communicated to the authors (W.G. Sanford, 1991, personal communication).

Plant indices of major mineral deficiencies

Nitrogen

Nitrogen is required by pineapple in greater amounts than any other nutrient except potassium. Providing adequate supplies of N to rapidly growing plants is essential to maintain high rates of growth and produce good yields. Both leaf size and number may decrease when nitrogen is deficient and fruit and crown mass are consequently reduced. Slips may be absent on plants that normally produce them. Plant indices for nitrogen include leaf colour and nitrate-nitrogen in leaf basal white tissue, total nitrogen in green tissue and leaf chlorophyll content. Soil indices for N, if used, only provide an indication of the N required for early growth of plants. Many tropical soils contain small amounts of nitrogen, so meeting crop N requirements is an important and challenging task.

Leaf colour is an important diagnostic index for nitrogen and is the most important index defined in the pineapple crop log of Nightingale (1942a). When N is deficient, leaves are yellowish green to yellow. However, symptoms in the field are different from those normally found in solution culture. Normally a well-exposed nitrogen-deficient plant will have yellow older leaves because the nitrogen in those plants is translocated to the younger leaves. In the case of nitrogen-deficient plants grown in the field, the older leaves remain green despite the removal of nitrogen from them because of mutual shading of lower and older leaves by adjacent plants. In the field, it is the younger leaves that are yellow. Thus, leaf colour is an integrated index that estimates the nitrogen requirement of pineapple on the basis of its relative carbohydrate status (Nightingale, 1942a; Table 7.2).

The colour indices defined for assessing plant nitrogen status are given below.

- No. 0 colour: yellow. Leaves having no. 0 colour (similar to Plate 15, right-hand leaf) are senescing or senescent and so are relatively inactive physiologically. A high percentage of leaves having no. 0 colour may be observed on newly planted slips and crowns during drought.

Table 7.2. Characteristics of the four ranges of pineapple leaf colour (after Nightingale, 1942a; Sanford, 1962).

Designation	Colour	Cell starch capacity (%)	Carbohydrate relative to N	Leaf texture
No. 0	Yellow	Variable	Variable	Variable
No. 1	Yellow-green	75–100	High	Stiff
No. 2	Olive-green	50–75	Intermediate	Soft–stiff
No. 3	Black-green	25–50	Low	Soft

- No. 1 colour: yellow-green (similar to Plate 15, second leaf from the right). These leaves are characteristic of those that are exposed to full sunlight. The cells of such leaves are filled with starch granules to within 75–100% of their total capacity. Consequently, the amount of carbohydrate in relation to protein nitrogen is high. The leaf texture of such plants is stiff and the leaves will break with a crackling sound when flattened. While additional nitrogen fertilizer could decrease the percentage of leaves with no. 1 colour, there is little evidence that vegetative growth over the first several months is restricted by lack of nitrogen.
- No. 2 colour: olive-green (similar to Plate 15, middle two leaves). Leaves that are olive-green in colour are associated with many different kinds of healthy pineapple crops grown in full sunlight. Cell starch capacity in these leaves is 50–75% of capacity.
- No. 3 colour: blackish-green (similar to Plate 15, left most two leaves). The leaves in this range are very dark green in colour with definite black overtones. Such leaves are characteristic of healthy plants grown in shade. Leaf texture is soft. In contrast to leaves having no. 1 colour, flattening of these leaves does not normally cause them to rupture. The cell starch capacity of these leaves is low relative to the amount of protein nitrogen.

The evolution of leaf colour on a growing 'Smooth Cayenne' plant during the crop development cycle in Hawaii (autumn planting with natural induction occurring 14 months later in the following winter) was described (W.G. Sanford, 1991, personal communication) as follows.

The leaves of crowns, slips or suckers prior to and immediately after planting in the autumn of the year become dehydrated and begin to senesce as the root system becomes established. For approximately the first 3 months after planting, no new leaves emerge so the visible leaves are primarily no. 0 colour or yellow. Such leaves are not physiologically active and will not become so after growth commences. As roots develop and new leaves appear, the fraction of leaves that are of no. 1 colour or yellow-green increases and these leaves are physiologically active. As plant leaf area expands and plants begin to shade each other, the older leaves will become no. 2 colour or olive-green due to this shading by younger leaves. At 6 months after planting, 40% of the leaves will exhibit no. 0 colour (all at the base of the plant) and 60% will have no. 1 colour (all at the top of the plant). By 10 months after planting, 25% of the leaves will be no. 1 colour (youngest leaves), 50% will be no. 2 colour (intermediate-aged leaves) and 25% of the leaves will be no. 3 colour (oldest leaves). By 14 months after planting, the upper and youngest leaves will be no. 1 colour (yellow-green), the intermediate leaves will be no. 2 colour (olive-green) and the lower and oldest leaves will be no. 3 colour (blackish-green) because of shading by the upper leaves and adjacent plants.

In Hawaii, experimental results have shown that the greatest responses to N fertilizer occur when plants are in the no. 1 and no. 2 colour ranges. For that reason, leaf colour estimates report the percentage of leaves exhibiting no. 1 colour, although during the early period of growth both no. 0 and no. 1 colours are combined in the visual estimate. In experiments where no. 1 colour readings ranged between 90 (mostly yellow-green) and 15% (mostly olive green) near the time of floral induction, in almost every case average fruit mass increased with added fertilizer N as the percentage of leaves having no. 1 colour decreased. In practice, a hypothetical trend line of decreasing leaf no. 1 colour readings with increasing plant age and increasing plant mass is followed (Sanford, 1962; Swete Kelly, 1993) and N is applied to maintain leaf colour on this hypothetical line. Thus, where foliar application of nitrogen is the practice, nitrogen fertilizer is applied in amounts and at frequencies approximately related to the increase in plant mass over time. Leaf no. 1 colour decreases and then increases after each nitrogen application, but the long-term objective is to decrease plant no. 1 colour readings to about 15% at the time of forced induction of flowering.

Since the use of no. 1 colour readings is based on greenness, which is in fact a measure of leaf chlorophyll content, any nutrient or other factor that influences leaf chlorophyll levels can interfere with the use of this index. Deficiencies of iron, magnesium and phosphorus are most likely to interfere with the use of this index because these deficiencies decrease leaf chlorophyll concentrations. Application of excessive amounts of herbicides can also reduce leaf chlorophyll levels. Therefore the successful use of no. 1 colour readings is dependent on eliminating, minimizing, or recognizing all factors other than nitrogen that can also influence leaf colour.

Young *et al*. (H.Y. Young, B.H. Krauss and W.A. Gortner, 1961, unpublished results, Pineapple Research Institute of Hawaii) proposed that measures of both chlorophyll and total leaf nitrogen would provide a more quantitative substitute for the leaf colour index. Chlorophyll and total nitrogen were measured on the middle one-third of the green tissue of 'D' leaves while whole-plant per cent no. 1 colour was estimated visually. Leaf chlorophyll decreased approximately linearly as 'D' leaf total nitrogen decreased, while the reverse was true for per cent no. 1 colour (Table 7.3). Other than via the use of the leaf colour index, no information was found to indicate that a chlorophyll-based index has been used to assess N nutrition in pineapple. Although a direct-reading chlorophyll meter exists, it is likely that plant-to-plant variations in chlorophyll would make it an unsuitable index of nitrogen sufficiency.

In terms of leaf N levels, a plant having 0.1% (1000 p.p.m.) or less nitrogen on a fresh-mass basis (1.2% or 12,000 p.p.m. on a dry-mass basis) in the middle third of 'D' leaves would be considered quite deficient. A similar N index based on whole 'D'-leaf analysis (Martin Prevel, 1959, 1970; Marchal *et al*., 1970; Lacoeuilhe and Gicquiaux, 1971a,b,c) assumes that, where N is less than 1%, growth will be limited by N and all N greater than 1% of leaf dry matter is assumed to be available for the growth of new tissues. Variations in nitrogen concentrations in successive 'D' leaves can be correlated with the growth of each 'D' leaf. The quantity of nitrogen available for growth can thus be determined in relation to the nitrogen content in the leaf. Leaf analyses made in a large number of fertilization trials showed that the critical mass of nitrogen

Table 7.3. Relationship between chlorophyll (mg kg^{-1} fresh mass) in the middle third of 'D'-leaf green tissue, total nitrogen (%, fresh-mass basis) in the same tissue and per cent no. 1 colour at two plant age ranges (H.Y. Young, 1961, Pineapple Research Institute of Hawaii, Honolulu, unpublished data).

	6–11 months		12–15 months	
Chlorophyll	Nitrogen	No. 1 Colour	Nitrogen	No. 1 Colour
400	0.35–0.40	15	0.32–0.36	0
380	0.31–0.34	25	0.28–0.31	10
360	0.29–0.30	30	0.26–0.27	15
340	0.27–0.28	35	0.24–0.25	20
320	0.25–0.26	45	0.22–0.23	30
300	0.23–0.24	55	0.21	35
280	0.22	65	0.20	45
260	0.21	70	0.19	55
240	0.20	75	0.18	60
220	0.19	85	0.17	70
200	0.17–0.18	95	0.15–0.16	75
180	0.15–0.16	100	0.13–0.14	80

Regressions:
Chlorophyll (C) and N, 6–11-month plants: $N = -0.01252 + 0.000879C$; $r^2 = 0.947$.
Chlorophyll (C) and N, 12–15-month plants: $N = -0.1673 + 0.000808C$; $r^2 = 0.943$.
Chlorophyll (C) and no. 1 colour (%), 6–11-month plants: $\% = 171.23 - 0.3907C$; $r^2 = 0.995$.
Chlorophyll (C) and no. 1 colour (%), 12–15-month plants: $\% = 149.49 - 0.3732C$; $r^2 = 0.995$.

required in the 'D' leaf at flower induction to obtain a fruit of 1.8 kg (without crown) was 100 mg (Marchal, 1975, as cited by Py *et al.*, 1987).

Nitrogen in soil is generally not measured, but, in Australia where farmers send their fruit to a cooperative cannery, soil nitrogen is measured as a means of helping to keep fruit nitrate levels below the 8.0 p.p.m. level considered to be critical for processed fruit. The optimum level of nitrogen in soil, based on water extraction after a 14-day incubation, is 120+ p.p.m. nitrate (NO_3), which is equivalent to 27 p.p.m. of N (Swete Kelly, 1993). The preplant nitrogen recommended is based on preplant levels of nitrate found in soil (Table 7.4). Total plant-crop requirements for nitrogen for pineapple range from 250 to 700 kg ha^{-1} (i.e. 4 to 10 g $plant^{-1}$), depending on the soil and ecology of the site, plant population density, expected fruit mass and other environmental or management factors. Calibration experiments, leaf colour indices and tissue indices can all be used to guide growers to the correct amount of nitrogen required for optimum growth. Details of fertilizer types and methods of application are discussed in Hepton (Chapter 6, this volume).

Table 7.4. Preplant nitrogen and potassium recommendations for 'Smooth Cayenne' pineapple in Australia with varying amounts of residual soil nitrate-nitrogen and potassium (Swete Kelly, 1993).

Preplanting level	Preplant application (kg ha^{-1})
Nitrogen	
125	0
100	20
75	45
50	70
25	95
0	100
Potassium	
150	0
120	75
100	125
80	175
60	225
40	275
20	325
0	375

Phosphorus

The growth of all plant parts is depressed as a result of phosphorus deficiency. However, the phosphorus requirement of pineapple is low and plants can extract P from soils having very low levels of that nutrient. The plants P requirements can almost always be met by applying P prior to planting. Soil P (modified Truog method) is the primary index used to assess the P requirement of pineapple, and levels of 20 p.p.m. or greater are adequate to sustain pineapple growth. The symptoms of P deficiency are observed at soil levels below 5.0 p.p.m. (Swete Kelly, 1993).

The visual symptoms of phosphorus deficiency are not commonly seen and are not particularly specific. They can be confused with plants suffering from root injury due to such causes as drought, nematode damage or mealybug wilt. Phosphorus-deficient plants have erect, long, narrow leaves. Older leaves show leaf-tip dieback preceded by a chlorotic or red-yellow area, which extends downward along the margins of the leaves. Young leaves, primarily because of the contrast, appear to be dark green but with considerable red pigment.

Plants with a phosphorus content of 0.009% (90 p.p.m.) or less, fresh-mass basis (0.108% or 1080 p.p.m. on a dry-mass basis), in the basal white tissue of the 'D' leaves will have the described symptoms. Phosphorus analysis of the basal white tissue of 'D' leaves was developed by Nightingale (G.T. Nightingale, 1946, unpublished results, Pineapple Research Institute of Hawaii) as the index for determining P fertilizer requirements. However, critical values are difficult to define because leaf P tends to decrease when growth is rapid. Mycorrhizal associations exist in pineapple roots (Mourichon, 1981). However, mycorrhizal fungi appar-

ently do not contribute significantly to the P nutrition of pineapple, except where soil P is extremely low, much less than 0.02 mg l^{-1} of soil solution (Aziz *et al.*, 1990), or in *in vitro* conditions (Guillemin *et al.*, 1997). In a recent study, which did not include data on P in soil or leaves, average fruit mass and yield per 12 m^2 plot were significantly greater where plants were inoculated with *Glomus mosseae* and *Glomus manihotis* (Thamsurakul *et al.*, 2000) relative to the control or to either mycorrhiza species alone. If mycorrhyzae did facilitate P uptake, they would only postpone the time when P fertilization would be required.

The leaf may not be as important as the soil as an index for P, but leaf analysis provides a check on the adequacy of soil supplies. Leaf P in the 'D'-leaf basal white tissue naturally increases with age – for instance, from 0.01% (100 p.p.m. in 'D'-leaf basal white tissue on a fresh-mass basis) at 5 months to about 0.02% (200 p.p.m.) at flower induction (Swete Kelly, 1993). According to Py *et al*. (1987), leaf P in the whole 'D' leaf should be 0.8% of dry matter at the time of flower induction.

Potassium

Potassium, like nitrogen, is required in large amounts to sustain pineapple plant growth. Potassium deficiency would decrease photosynthesis and thus plant growth, fruit mass and slip production (Swete Kelly, 1993). With potassium deficiency (Plate 16), fruits have reduced sugar and acid levels and have a pale colour (Py *et al.*, 1987; Swete Kelly, 1993), presumably because of reduced carotenoid development. Where K is deficient, the fruit peduncle diameter is reduced (Py *et al.*, 1987), the peduncle is weak (Swete Kelly, 1993) and fruits are more prone to lodging and sunburn and have lower acidity and aroma development.

As with phosphorus, the primary index for K is the level in the soil, because K is well retained by most soils. The optimum soil level at planting is 150 p.p.m. and potassium deficiency symptoms are observed when the soil level is below 60 p.p.m. (Swete Kelly, 1993). The soil level in p.p.m. and the recommended amount of preplant K is shown in Table 7.4.

The high requirement of pineapple for potassium has made it relatively easy to reproduce deficiency symptoms. Low levels of potassium are associated with shorter leaves that are narrower in relation to their length, growth is reduced, necrotic spots can be seen in the green photosynthetic tissue (chlorenchyma) of the leaves and leaf tips die back (Py *et al.*, 1987; Swete Kelly, 1993). During the early stages of potassium deficiency, leaves are dark-green and narrow (Plate 16), but, if the deficiency is prolonged, leaves eventually become yellow.

Potassium analysis is done on the basal white tissue of 'D' leaves (Swete Kelly, 1993) or whole 'D'-leaf samples (Py *et al.*, 1987). Visual potassium deficiency symptoms are evident when there is less than 0.20% K (2000 p.p.m.), fresh-mass basis (2.4% on a dry-mass basis), in the basal white tissue of 'D' leaves. The critical leaf K level at flower induction is reported to be 0.30% (3000 p.p.m.) on a fresh-mass basis (3.6% on a dry-mass basis) for basal white tissues (Swete Kelly, 1993; W.G. Sanford, personal communication) or 2.2–3% for the whole 'D' leaf on a dry mass basis (Dalldorf and Langenegger, 1976; Py *et al.*, 1987). Swete Kelly (1993) recommends that leaf K of plants 3–5 months old should range between 3500 and 4000 p.p.m. (basal white, fresh-mass basis).

Calcium

Pineapple has a very low requirement for calcium, but deficiencies can occur on highly weathered soils low in basic cations and on soils where pH has been lowered by long-term use of acidifying fertilizers, such as ammonium sulphate. For optimum growth, soils should contain greater than 100 p.p.m. of Ca, a level approximately one-tenth that normally recommended for most crops, and deficiency symptoms are observed when the level is less than 25 p.p.m. Calcium is commonly applied to amend soil pH as well as to supply Ca, but, in many areas, the soil pH is kept at or below 5.5 to limit the incidence of heart and root rots caused by *Phytophthora* spp. Since the amount of cal-

cium required to adjust pH varies with soil cation exchange capacity, the lime requirement should be based on a lime titration curve developed specifically for each soil type in which pineapple is grown. Gypsum can be used where it is desirable to supply calcium without changing soil pH. However, only one reference (Hartung *et al*., 1931) was found indicating that gypsum might have been evaluated as a source of calcium for pineapple.

Visual symptoms of calcium deficiency on vegetative (Plate 17) and reproductive plants (Fig. 7.2) were documented at the Pineapple Research Institute of Hawaii (Sanford, 1961), both in sand culture and in the field. Sanford (W.G. Sanford, personal communication) observed that leaf colour of calcium-deficient plants was abnormal, a grimy grey-green rather than the more normal clean yellow-green or green. The initial growth of calcium-deficient pineapple plants may not be stunted, but as the deficiency becomes more severe, growth depression is very evident. Calcium deficiency symptoms, as with those of boron, are most likely to be seen initially on the fruit because the demand for both calcium and boron in the growing point is highest at the time of floral differentiation. When Ca deficiency is severe, cells at the growing point fail to divide and other cells tear apart because of weak cell walls, so new leaves may appear to be cut off or tipless, with serrations or scalloping along the margins, and leaves may develop callus, be abnormally thick and have streaks of corky tissue running parallel to their length. With extreme deficiency, the growing point may die, resulting in the growth of side-shoots, which may be initially symptom-free. In some cases, plants fail to produce an inflorescence and continue to grow vegetatively. In this case, the leaves become progressively shorter as they develop. Roots are thicker than normal and, as a result, such plants are more difficult to pull out of the ground than a normal plant. Fruits may be abnormal in size and shape. Symptoms have been

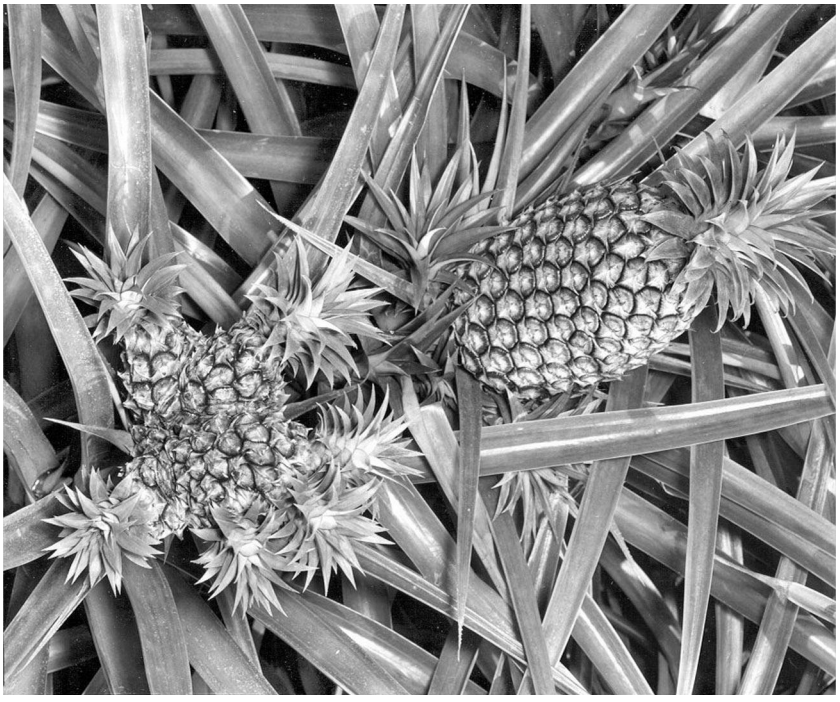

Figure 7.2. Multiple fruit of 'Smooth Cayenne' pineapple resulting from severe calcium deficiency (photo courtesy of W.G. Sanford).

observed only for plants having a concentration of 0.002% or less, fresh-mass basis (0.024%, dry-mass basis), in the basal white tissue of the 'D' leaf. The critical concentration at flower induction is 0.015% fresh mass (0.18%, dry-mass basis) in the basal white tissue, and deficiency symptoms develop when the level is less than 0.004% (Swete Kelly, 1993). In the whole 'D' leaf, leaf Ca should be 0.10% of dry matter at the time of induction (Py *et al.*, 1987).

Magnesium

Magnesium is a component of the chlorophyll molecule, and a deficiency will reduce chlorophyll concentration, photosynthesis and growth. This nutrient is mobile in the plant and the predominant visual symptom of magnesium deficiency is bright yellow older leaves (Plate 18), particularly those leaves or parts of leaves exposed to sunlight. Such leaves will frequently have bands of green that run diagonally across the leaf as a result of being shaded by leaves above them (Py *et al.*, 1987; Swete Kelly, 1993). Sanford (W.G. Sanford, personal communication) notes that the symptoms of Mg deficiency are most pronounced just prior to floral differentiation and all leaves may be yellow during fruit development. The stems of Mg-deficient plants are short and have a small diameter. The root systems tend to be weak, so magnesium-deficient plants are easily pulled from the soil. Fruits are reported to be low in acidity, sugar content and aroma (Py *et al.*, 1987). This symptom probably reflects the plant's reduced capacity to assimilate CO_2 via photosynthesis.

At planting time, the optimum level of Mg in soil is 50 p.p.m. and Mg deficiency occurs at levels below 10 p.p.m. (Swete Kelly, 1993). Swete Kelly (1993) states that deficiency symptoms begin to develop when Mg in the basal white tissue of 'D' leaves reaches 0.015% fresh mass (0.18%, dry-mass basis) and symptoms are present when the Mg content in the basal white tissue of 'D'-leaves is 0.009% or less, fresh-mass basis (0.108%, dry-mass basis). The critical concentration in fresh 'D'-leaf basal tissue at floral induction is reported to vary from 0.025% (in low-potassium soils) to 0.027% (in high-potassium soils) (0.30% and 0.32%, respectively, dry basis) (Swete Kelly, 1993). Magnesium in the whole 'D' leaf should be 0.18% of dry matter at the time of induction (Py *et al.*, 1987).

Sulphur

Sulphur deficiency is rare, probably due to the fact that many fertilizers contain sulphates. Deficient plants have bright lemon-yellow leaves that are broader than normal. As contrasted with magnesium deficiency, where chlorosis occurs mainly on older leaves, both young and old leaves of sulphur-deficient vegetative plants are yellow. As the deficiency progresses, later-formed leaves become narrow, plants are stunted and fruit size is reduced (Py *et al.*, 1987). The symptoms described above were associated with a sulphur level of 0.005%, fresh-mass basis (0.06% on a dry-mass basis) in the middle third of 'D' leaves.

Iron

Iron is an immobile nutrient so iron-deficiency symptoms always appear first on young leaves. In Hawaii, a visual index was developed based on the percentage of the leaf area ('B' through 'F' leaves only), if any, that exhibited chlorotic mottled areas characteristic of this deficiency (W.G. Sanford, personal communication), and this index has also been adopted in Australia (Swete Kelly, 1993). Total iron in the middle third of 'D'-leaf green tissue expressed on a fresh-mass basis was also used in Hawaii as an index for determining iron requirements. Where the 'D'-leaf level is 8 p.p.m. or higher in the absence of high levels of soluble manganese, visual iron deficiency is 40% or lower, a level considered adequate for maximum growth. In the presence of soluble soil Mn, the iron content of leaves is not well related to the existence of deficiency symptoms. Also, unlike the situation with other nutrients, pineapple plants can show visual symptoms of iron deficiency with no decrease in yield.

Where soluble manganese is high – a common situation in soils having high man-

ganese and low pH – the ratio of soluble iron to soluble manganese in the soil and in the whole 'D' leaf is more important than the absolute amounts of either element (Hopkins *et al.*, 1944). Py *et al.* (1987) report that iron deficiency occurs and visual symptoms are observed where iron in the 'D' leaf is between 60 and 475 p.p.m., dry-mass basis, and the Fe:Mn ratio is less than 0.4. Manganese deficiency occurs and visual symptoms are observed if Mn in the 'D' leaf is between 29 and 78 p.p.m., dry-mass basis, and the Fe:Mn ratio is greater than 10.5. Iron deficiency has been observed in Queensland, Australia, when cold, wet soils prevent the uptake of iron or where roots have been damaged by pests (Swete Kelly, 1993).

Visual symptoms of iron deficiency on pineapple grown in Hawaii were first described by Johnson (1916). The initial symptoms appear as interveinal chlorosis of the younger leaves; leaf veins, which run parallel to the length of the leaf, remain green whereas the areas between the veins are yellow-green or yellow. When the deficiency is mild, the leaves become yellow, with green mottling (Swete Kelly, 1993). As the deficiency becomes more severe, the entire surface of the leaves may be pale yellow (Plates 19 and 20) or creamy white, with considerable red pigmentation at the terminal ends. Such leaves are also soft and leathery, rather than rigid, and have considerable tip dieback. Plants with severe iron deficiency will have fruit that are small, hard and reddish in colour and with cracking between the fruitlets. The crowns will be light yellow or creamy white in colour. In the absence of high soluble manganese levels, severe deficiency symptoms have been associated with 3.0 p.p.m. or less of iron, on a fresh-mass basis (36 p.p.m. on a dry-mass basis), in the middle third of 'D' leaves. As noted above, with high levels of soluble manganese, the ratio of iron to manganese is more critical than the absolute amounts of either element. Iron sulphate sprays, often applied biweekly, are used to correct the deficiency. To be effective, the iron in iron sulphate sprays must be applied in reduced form, and good storage conditions are required to prevent oxidation.

Zinc

Zinc deficiency can occur in soil with a pH of 6.0 or higher, with low organic-matter content (observed in Hawaii in such conditions) or where lime or phosphorus were not well incorporated or were applied in excessive amounts (calcium- or phosphorus-induced zinc deficiency). Zinc deficiency is widespread in Queensland, Australia (Swete Kelly, 1993), especially on previously uncultivated land. The deficiency has also been observed in Hawaiian soils that have low native fertility. When the deficiency is severe, the plant's central cluster of leaves is curved (crook-neck) (Plate 21), especially with younger plants (Swete Kelly, 1993). When the deficiency develops in older plants, the surfaces of the leaves develop yellowish-brown, blister-like (elevated) spots. The centre leaves may on occasion have rips or serrations on their edges. In less severe cases, the blisters occur only on the older leaves and the centre leaves are only slightly curved. Occasionally, the curved leaves will be seen without blisters. At times, zinc-deficient plants, like calcium-deficient plants, have been observed to remain continuously vegetative. Zinc deficiency is distinguished from calcium deficiency by the curved central leaves and the presence of blisters on the leaf surfaces. Zinc concentration in the 'D' leaf is not diagnostic of zinc deficiency. A level of 4 p.p.m., fresh-mass basis, in the stem apex is considered adequate and 3.0 p.p.m. or less, fresh-mass basis (36 p.p.m. on a dry mass basis), in the stem apex will be associated with typical zinc-deficiency symptoms. The deficiency is easily correctable with sprays of zinc sulphate.

Boron

Boron deficiency has not been observed in Hawaiian pineapple fields, but has been observed in Australia, Côte d'Ivoire, Costa Rica, Honduras, Martinique and the Philippines. Boron deficiency in leaves and fruit was induced in sand culture (D.H. Smith, B.H. Krauss and K. Pfenninger (1962) *PRI News* 10, 95–97; D.H. Smith, B.H. Krauss and K. Pfenninger (1965) *PRI News* 13,

263–274; unpublished results, Pineapple Research Institute of Hawaii), with the symptoms being first observed on the fruit. Fruitlets of immature fruit showing boron deficiency appear glossy and green in contrast to the scurfy, dull and whitish appearance of a normal fruit at this stage. The glossy appearance is due to the absence of trichomes (multicellular plant hairs). As the fruit develops, small, shallow cracks appear between the fruitlets and within 2 weeks these cracks become corky (see Fig. 9.29). Fruit borne on plants having severe boron deficiency are much smaller than normal fruit, and multiple crowns are also reported (Py *et al.*, 1987). The symptoms of boron deficiency seen on fruit may be similar in some conditions to the symptoms of interfruitlet corking caused by *Penicillium funiculosum* (see Rohrbach and Johnson, Chapter 9, this volume).

The symptom of boron deficiency on vegetative leaves, if it occurs, is death of the tips of the youngest leaves, sometimes with serrations on the margins. In extreme cases, death of the growing point will occur. In such a plant the central leaves will be stiffer and shorter than normal and lateral buds will eventually develop. The symptoms of boron and calcium deficiency on vegetative plants are similar. As in the case of calcium, the initial symptoms of boron deficiency in the field are most likely to be observed on the fruit rather than on vegetative plants, because the greatest demand for both boron and calcium is at the growing point as it shifts from the production of vegetative structures to reproductive ones. Symptoms of boron deficiency can be expected to occur when boron is 0.2 p.p.m. or less, on a fresh-mass basis (2.4 p.p.m. on a dry-mass basis), in the middle third of 'D' leaves approximately 10 months after planting. Fruit symptoms were associated with a level of 0.4 p.p.m. or less boron in the middle third of the longest crown leaves 4.5 months after floral differentiation. In Australia, boron deficiency is prevented by forcing of flower induction with sprays that contain 0.5% borax. Borax provides a source of B as well as raising the pH of the ethephon solution to about 9.0 to enhance its effectiveness, especially when warm temperatures make induction difficult (Sinclair, 1994).

Manganese

Manganese deficiency is rare and occurs in soils high in calcium with a high pH. Py *et al.* (1987) report that manganese deficiency symptoms are not specific. Affected leaves are marbled with pale green areas, mainly where vessels are located. Despite the presence of high levels of soluble manganese in many tropical soils, including those in Hawaii, symptoms of manganese toxicity have not been observed. Pineapple growing in acid soils tolerates high levels of both soluble manganese and aluminium where other plants show symptoms of toxicity. In acid, high-manganese soils, high levels of soluble manganese appear to interfere with iron absorption and translocation (Sideris, 1950) or utilization. As noted above, the iron : manganese ratio is more important than the absolute amount of either element.

Copper

The leaves of plants deficient in copper are lighter green than those of normal plants and are distinctly U-shaped in cross-section relative to normal leaves. Tips of leaves curve downward instead of being erect. The deficiency is common in the heavily leached sandy soils of southern Queensland, Australia (Swete Kelly, 1993), and has also been observed in Malaysia on peat soils. The optimum range in the 'D'-leaf basal white tissue is 10–50 p.p.m. on a fresh-mass basis. Copper deficiency is easily corrected with a copper sulphate spray.

Molybdenum

There are no known reports of visual symptoms of molybdenum deficiency on pineapple and also little indication of a pineapple growth response to Mo. Molybdenum is essential for proper functioning of the nitrate reductase enzyme, and it was reported that application of Mo can reduce the nitrate level in fruit juice (Chairidchai, 2000). Much additional work in Queensland, Australia, has failed to demonstrate any change in juice nitrate levels as a result of spraying plants with Mo (Scott, 2000).

Deficiency problems

Deficiencies of the macronutrients N, P, K, Ca and Mg are likely to occur anywhere that pineapple is grown if quantities removed by the crop and lost by leaching are not replaced through fertilization. Deficiencies of S and of the micronutrients Fe, Zn, B, Mn, Cu, Mo and Cl are likely to be localized in specific areas where pineapple is grown. The sulphur requirement of pineapple, which probably is as high as that for P, will be met by S-containing fertilizers if iron, potassium and zinc sulphate are applied to pineapple fields, though this situation could change if the application of these fertilizers is reduced or eliminated. Since the main function of Mo in higher plants is related to nitrate reduction, there is little chance that a Mo deficiency will occur in pineapple in most regions because most N taken up by pineapple is in the form of ammonium or urea, both of which can be absorbed through the leaves. However, Mo deficiency, at least in terms of insufficiency to reduce plant-absorbed nitrate, has been reported in Thailand (Chongpraditnun *et al.*, 2000). Boron and copper deficiency are already found in a few countries and these two nutrients may eventually become limiting in other pineapple-growing regions. Iron deficiency is common in many pineapple growing regions while zinc deficiency seems to be somewhat less widespread.

As long as fertilizers are readily available and inexpensive relative to the value of the crop and the technology is available to apply these fertilizers after the deficiencies appear, deficiencies of most nutrients should not limit the productivity of pineapple where the crop is grown for commercial purposes. This is because most deficiencies are readily correctable by foliar application of soluble sources of nutrients. The pineapple plant is ideally suited for foliar fertilizations and most nutrients are readily absorbed through the leaves or are taken up when solutions containing essential nutrients flow to the leaf axils, where roots commonly exist to absorb them.

Plant Requirements

Nutrients removed by the crop

Nutrients are exported from the field in fruits and crowns, slips, suckers and other propagules harvested for planting material. Hence, the amounts of exported nutrients are related to fruit and propagule yields. Mineral contents of fruits, in per cent, are reported to be in the range 0.075–0.08 N, 0.015 P_2O_5, 0.2–0.26 K_2O, 0.015–0.02 CaO and 0.13–0.18 MgO on a fresh-mass basis (Py *et al.*, 1987). The quantity and extent of variation in quantities of essential nutrients immobilized in fruits and propagules removed from fields are considerable (Table 7.5).

Crop residue

Significant vegetative residue remains at the end of the pineapple cycle and the amount

Table 7.5. Amounts of nutrients removed by crowns, fruits and suckers (data from Martin-Prevel, 1961a,b,c,d; Martin-Prevel *et al.*, 1961; Py *et al.*, 1987).

		Nutrients (kg ha^{-1})				
Organ	Fresh mass (g)	N	P_2O_5	K_2O	CaO	MgO
Crown*	205	19	11.5	59	8.5	10.5
Crown*	295	28	15.4	89	11.9	13.0
Crown†	390	36	20.2	111	29.3	16.5
Fruit‡		43	16.5	131	17.0	10.0
Sucker‡		24.5	8.0	43	10.0	6.2

*Côte d'Ivoire, 5.5 plants m^{-2}.
†Martinique, 5.5 plants m^{-2}.
‡3.8 plants m^{-2}.

and the quantity of nutrients it contains is determined, at least in part, by the quantity of fertilizer applied during the crop cycle. This residue can vary from about 70 to 240 t ha^{-1} on a fresh-mass basis or 40–60 t ha^{-1} on a dry-mass basis (Py *et al*., 1987; Pena Arderi and Dominguez Martin, 1988; W.G. Sanford, 1990, personal communication). Pineapple residue is approximately 75% leaves and 25% stems, with the root system representing a relatively insignificant amount. Most of the dry residue consists of organic compounds, such as sugars, starch, cellulose and proteins. The residue contains, in per cent, approximately 1.0 N, 1.0–2.0 K and approximately 0.1–0.4 P, Ca, Mg and S and much smaller amounts of Fe, Zn, B, Cu, Mn and Mo, though values can range rather widely at the end of the crop cycle (Table 7.6). The incorporation of the residue could return substantial amounts of organic matter to the soil, as well as contributing significant amounts of nutrients to a subsequent crop of pineapple.

The supply of plant nutrients from the residue to a subsequent pineapple crop depends on how the residue is handled. Chopped green tops of pineapple are a good source of roughage for ruminant animals (Henke, 1934; Anon., 1944; Bishop *et al*., 1965; Wayman *et al*., 1976; Li, 1978; Stanley and Ishizaki, 1979) and, if harvested for this use, will also remove large amounts of plant nutrients from the field. Since most of the nutrients accumulate in the green leaves, the nutrients lost in harvested leaves would be

Table 7.6. Inorganic nutrient content of pineapple plant residue at the end of the crop cycle.

Element	Concentration (% dry weight)	Average nutrient content in a given amount of residue (kg ha^{-1})		
		30 t ha^{-1}	50 t ha^{-1}	70 t ha^{-1}
Wayman *et al*., 1976				
N	0.78 ± 0.13	234	390	546
K	0.94 ± 0.43	282	470	658
P	0.07 ± 0.01	21	35	49
Ca	0.43 ± 0.21	129	215	301
Mg	0.16 ± 0.03	48	80	112
S	0.23 ± 0.09	69	115	161
Mn	0.05 ± 0.01	15	25	35
Fe	0.04 ± 0.01	12	20	28
Cu	0.003 ± 0.001	0.9	1.5	2.1
Si	0.32 ± 0.19	96	160	224
Na	0.01 ± 0.01	3	5	7
Cl	0.36 ± 0.05	108	180	252
Al	0.13 ± 0.08	39	65	91
Maui field (Ingamells, 1981)				
N	1.03	309	515	721
K	1.94	582	970	1358
P	0.19	57	95	133
Ca	0.31	93	155	217
Mg	0.19	57	95	133
S	0.07	21	35	49
Mn	0.027	8.1	13.5	18.9
Fe	0.018	5.4	9	12.6
Cu	0.001	0.3	0.5	0.7
Zn	0.003	0.9	1.5	2.1
Si	0.31	93	155	217
Na	0.08	24	40	56
Al	0.029	8	14	20

considerably greater than the fraction of plant mass removed. Burning the residue rather than incorporating it into the soil will volatilize most of the N and S, while all other nutrients will be converted to soluble inorganic forms. Nutrients in soluble form are readily available to a subsequent crop, but are also subject to leaching by rainfall.

Pineapple residue that was chopped and then incorporated into the soil decomposed in approximately 26 weeks in Hawaii (Table 7.7). Early in the decomposition process, much of the N and probably some of the S and P would be utilized by microorganisms involved in the residue decomposition process. Consequently, the available N and P decreased during the period of rapid residue decomposition (Table 7.7). On the other hand, available K, which is primarily present in free (unbound) form in plant tissue, steadily increased during the decomposition period.

The elements Ca and Mg, which are primarily in organic form in the residue, are released later than K. Ingamells (1981), who compared the growth of pineapple in four soil series with and without pineapple residue, reported that the incorporation of residue into the soil immobilized N for 30–60 days, after which its availability increased. In the Hawaii environment, this initial reduced availability would be of little consequence, because roots do not begin to proliferate through the soil until 30 or more days after planting. The change in availability of N had no significant effect on the concentration of the N in the pineapple plants grown in the soil. At 16 weeks after planting, plants grown in soil in which residue had been incorporated had higher concentrations of K, Cl, Ca, Si, Mg, P and S in pineapple leaves than did plants grown in soil with no residue (Ingamells, 1981). Since the incorporation of pineapple residue into the soil also increased the moisture-holding capacity of the soil, the increase in the level of these elements in plant leaves may be due to the combination of a higher level of these nutrients and greater available soil moisture.

The benefits from the incorporation of residue into the soil are difficult to evaluate, especially for a long-term crop like pineapple grown in the tropics, where there is ample time during the crop cycle for complete decomposition of the residue. As with any incorporated organic matter, pineapple residue can improve soil physical, chemical and biological characteristics, but a direct effect on the following crop may not be obvious. In a study of residue management on a ferralitic sandy soil in Côte d'Ivoire, residue was incorporated, burned or mulched (Godefroy, 1979). The plants were spray-fertilized with N (amount not given) and 1000 kg ha^{-1} of K_2O. Nitrogen losses where high – approximately 200 kg ha^{-1} – in

Table 7.7. Effect of time on pineapple trash residue decomposition and nutrient availability (Tam and Magistad, 1936).

Weeks	Residue (tons per acre)	Extractable nutrients (mg kg^{-1} soil)		
		N	P	K
0	60.6	40	5	129
5	46.0		4	136
7	64.7	34		
9	55.7		3	165
11	58.4	29		
13	25.8		3	192
15	23.1	25		
19	12.4	24		
23	10.1	20		
29	5.6	27	7	352
35	6.7	36	6	403

all treatments. Potassium losses due to leaching were lower than for nitrogen, averaging, in kg ha^{-1}, 189 where residue was incorporated, 137 where it was burned and 107 where it was mulched.

Nutrient absorption and growth

Pineapple plant nitrogen and potassium requirements are low until about 4 months after planting (Lacoeuilhe, 1978; Ingamells, 1981), after which requirements increase with growth until flower induction. In an experiment where 8 g of N and 20 g of K_2O were provided for each plant prior to forcing, at the time of forcing at 10 months after planting plants of 375 g dry mass contained 5 g N and 11 g K (Lacoeuilhe, 1978). Plant nitrogen content remained constant during the period from forcing until harvest. However, K absorption continued to increase from forcing to harvest, and 13 g were accumulated in a plant dry mass of 800 g (Lacoeuilhe, 1978). Factors that reduce potential growth, such as drought, low temperature and root anoxia, reduce the plant's nutrient requirement (Py *et al*., 1987).

Total uptake of a particular nutrient does not necessarily indicate a plant's requirements for that nutrient. Pineapple plants may take up more, the same as or less than the amounts required for optimum growth, depending on the factors indicated above and the specific nutrient in question. In a field high in available N and K, total uptake over a 30-month period was highest for K, followed by N and phosphorus. The efficiency of pineapple in extracting K from the soil is high and, if readily available, the plant accumulates K in greater amounts than are required for optimum growth, often referred to as luxury consumption.

The uptake of nitrogen also shows luxury consumption, generally being proportional to the amount of nitrogen fertilizer applied during vegetative growth (Scott, 1993). Juice nitrate is an important quality factor in canned pineapple because high levels detin cans; 8 p.p.m. is considered the critical level in Australia (Scott, 1994). In Thailand, fruits that exceed 25 p.p.m. nitrate in the pineapple juice are rejected at the cannery (P. Chairidchai, 2000, personal communication). Juice nitrate levels can be highly correlated with nitrogen applied with fertilizers (Scott, 1993). In one study, juice nitrate averaged 1.0, 6.0 and 23 p.p.m. when N applied was 200, 600 and 1200 kg ha^{-1} (Scott, 1993). Heavy N fertilization and application of N fertilizers after flowering is more likely to result in elevated fruit nitrate levels (Chongpraditnun *et al*., 1996). However, nitrate levels in leaves sampled at different stages of plant growth were not well correlated with juice nitrate levels (Scott, 1994). Fruit from plants with a low level of molybdenum in the 'D' leaf had a high nitrate content in juice in Thailand (Chairidchai, 2000; Chongpraditnun *et al*., 2000). In these experiments, high fruit nitrate content and low 'D'-leaf molybdenum content were thought to be due to increased absorption of molybdenum by soil particles at the low soil pH.

Luxury consumption of calcium (Godefroy *et al*., 1971), magnesium, sulphur, boron, chlorine, copper and manganese also occurs in pineapple when these elements are readily available, whether they are taken up from the soil or applied to the leaves in nutrient solutions (W.G. Sanford, personal communication). Conversely, low amounts of phosphorus are extracted by the plant and uptake is not proportional to the supply available, but reflects the plant's requirement for P. The levels of iron, zinc and molybdenum also do not generally increase with the available supply, but reflect the plant's requirement for these nutrients. However, as was noted above, leaf levels of iron and manganese can be above 500 mg kg^{-1} dry mass in soils that have a low pH (3.5–4.5) and high levels of soluble manganese.

Other elements that are accumulated by pineapple plants when levels are high in the soil are silicon, sodium and aluminium (Table 7.6). In Hawaii, relatively high concentrations of Na and Cl are found in soils in close proximity to the ocean, where sea-water sprays are prevalent (Sideris and Young, 1954; Sideris, 1955). Sea-water sprays can cause leaf-tip dieback, characterized by alternating dark brown and light brown bands running perpendicularly to the length

of the leaves (Sideris, 1955) and it was concluded that chloride in the spray rather than in the soil is the cause of leaf dieback. High levels of Cl in the soil can also result from the application of potassium chloride fertilizer to the soil and from soil fumigants, such as dichloropropene, which contain large amounts of chlorine. Leaf injury was not observed in soils high in Cl, perhaps due to the fact that the Cl taken up by the roots remains diluted in the plant, while sea spray concentrates on the leaves as the spray dries, causing salt injury. Salt injury on pineapple leaves was also not observed in response to increasing sodium chloride in the soil in pot studies (Wambiji and El-Swaify, 1974, 1976), even though leaf concentrations of both Na and Cl increased and growth decreased slightly. However, in a recent study (Marinho *et al.*, 1998), where plant establishment and early growth at 25°C were studied at salinity levels in irrigation water of 0–7 dS m^{-1}, establishment and growth were greatly reduced at salinity levels above 3 dS m^{-1}.

Nutrients and environmental quality

When growers strive for maximum production, the use of large amounts of fertilizer can result in nutrient losses, especially nitrate losses, in drainage water. A recent study of nitrate leaching in pineapple (Reinhart, 2000) showed that the loss of nitrate below a depth of 30 cm was greatest where large amounts of N (more than 300 kg ha^{-1} applied to a soil with high residual nitrogen) in inorganic fertilizer were applied prior to planting. Losses were negligible where manure was used in lieu of inorganic fertilizer (Reinhart, 2000). Foliar fertilization with over 700 kg N ha^{-1} did not increase leaching losses. Chemical losses through runoff and soil loss may also be significant when pineapple is cultivated on ridges on slopes without soil cover. They reached 63 kg N ha^{-1} $year^{-1}$, 44 kg K ha^{-1} $year^{-1}$ and 56 kg Ca ha^{-1} $year^{-1}$ in an experiment on volcanic soils in Martinique (Khamsouk, 2001). Nitrogen losses due to leaching, runoff and erosion may be an important problem, especially in tropical islands, such as Hawaii and the Caribbean, which have fragile ecosystems. Further studies are needed to better understand and predict nitrogen dynamics in pineapple cropping systems.

Effect of nutrition on fruit quality

Assuming that no other factors limit growth, the adequacy of the nutrient supply determines the plant growth rate, the plant mass at induction and ultimately the fruit mass at harvest. However, the plant-mass–fruit-mass relationship is by no means direct, as environment and the quality of forced induction are also important (see Bartholomew *et al.*, Chapter 8, this volume). The literature seems to indicate that plants well supplied with nutrients at the time of induction are likely to have larger fruit than plants of the same mass that have less than optimum nutrition (Py *et al.*, 1987). If nutrition is adequate at the time of induction, additional nutrients are typically not applied after that time, because nutrient absorption, except for potassium, ceases (Py *et al.*, 1987). Fruit mass is well correlated with plant mass at induction, and fruit quality is primarily determined by environmental factors. Where nutrient supplies at the time of induction are inadequate, fruit mass may be increased and fruit quality can be affected by the application of fertilizers after induction has occurred. Since fruitlet numbers are fixed soon after induction, fruit mass is only increased to the extent that additional nutrients result in an increase in fruitlet size. The focus of the following discussion relates mainly to the effect of nutrition on fruit quality.

Nitrogen

According to Py *et al.* (1987), N and K are the most important elements influencing fruit mass and quality in relation to each other and in relation to climate. It is not always possible to distinguish between the specific effect of N on fruit quality and its more general effect on overall plant growth and health. Hence, an increase in N increases the diameters of the core and the peduncle and the length of the peduncle. As a result, with

excess N, there is an increased risk of lodging and fruit sunburn (Py *et al.*, 1987). Nitrogen might also increase the number of double or multiple crowns (Gonzalez-Tejera and Gandia-Diaz, 1976) and increase the fragility and translucency of the flesh and the susceptibility to green ripe fruit (Lacoeuilhe, 1978). An increase in N resulted in a reduction in free acids (Marchal *et al.*, 1970; Gonzalez-Tejera and Gandia-Diaz, 1976; Py *et al.*, 1987), but may or may not reduce fruit total soluble solids (TSS). Cannon (1957) reported that fruit TSS decreased with increasing N when K was optimum but had no effect when K was sub-optimum. As was noted above, fruit nitrate content increases with increasing N (Scott, 1993, 1994), especially if plants are fertilized with N at or after induction of flowering.

Phosphorus

Phosphorus was reported to have a slight or no effect on fruit quality (Magistad and Linford, 1934b; Linford *et al.*, 1935) and also to decrease TSS and acidity but to increase ascorbic acid content (Tay *et al.*, 1968; Mustaffa, 1989). Because of the dominant role of P in growth, rather than in photosynthesis, as is the case for N and K, it seems likely that the effect of P on fruit quality will be small.

Potassium

Essentially all studies of the effect of K on fruit quality show that increasing levels of K increased fruit acidity, TSS, ascorbic acid and flavours and aroma (Magistad and Linford, 1934a,b; Cannon, 1957; Su, 1958; Tay *et al.*, 1968; Marchal *et al.*, 1970; Gonzalez-Tejera and Gandia-Diaz, 1976; Py *et al.*, 1987). There may be a decrease in the ratio TSS:titratable acidity, which is an important measure of eating quality (Smith, 1988), because acidity increases relatively more than TSS (Py *et al.*, 1987). The overall response to increasing available K is completely consistent with the specific role of K in the opening and closing of plant stomata, which regulate gas exchange, including the absorption of CO_2 during photosynthesis.

Calcium

Calcium supply affected fruit aroma, possibly because higher levels of Ca could interfere with the absorption of K, so the effect is probably not specific. Higher levels of Ca in the fruit are also associated with reduced incidence of storage disorders (Wilson Wijeratnam *et al.*, 1996; Selvarajah *et al.*, 1998).

Magnesium

Magnesium had no effect on fruit quality on peat soil (Tay, 1974; Gonzalez-Tejera, 1975), while Py *et al.* (1987) stated that its effect on fruit aroma was comparable to that of K. Garcia (1983) found an increase in TSS in the fruit of 'Red Spanish' pineapple due to application of magnesium.

Iron

In the only study of the specific effect of iron on fruit quality found, Linford (1934) reported that improving iron nutrition increased fruit translucence.

Conclusions

Comprehensive information on the nutrient requirements of 'Smooth Cayenne' pineapple exists, but the same quality and quantity of information are not available for most other varieties of pineapple. The ideal soil and tissue nutrient levels have been developed for this variety and in many areas they are used to guide the application of fertilizers, especially where intensive farming practices are used. Such practices represent the ideal situation, as they allow for the maintenance of optimum plant nutrition while minimizing the hazards to environmental quality of overfertilization. Such information is or will be needed for the other important cultivars and for any new hybrids that have different nutrient requirements from those of 'Smooth Cayenne'. Very large amounts of N and K are applied to pineapple where cultural practices are intensive. Potassium is usually retained well by most

soils and losses by leaching do not represent an environmental hazard. The fate of the large amount of N applied to pineapple remains insufficiently known and more work should be done to understand the nitrogen dynamics of pineapple-based cropping systems. Studies are needed to demonstrate that the large amount of nitrogen applied to the well-managed pineapple crop does not contaminate groundwaters with nitrate. It is likely that environmental concerns will eventually require that farmers manage nutrients in a way that protects both ground- and surface waters from nutrient contamination.

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8 Inflorescence and Fruit Development and Yield

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Introduction

The reproductive phase of the pineapple begins in response to natural or plant-growth-regulator-forced induction of reproductive development (natural induction and forcing). Because the inflorescence of pineapple is terminal, when reproductive development begins, formation of new leaves ceases. Expansion of previously initiated leaves continues, but not all of these expand fully. Some are found on the fruit peduncle and their size is much reduced relative to older fully expanded leaves.

Once reproductive development is initiated, inflorescence and fruit development continue without interruption until the fruit matures, although development may be interrupted by disease or slowed by water or temperature stress. Fruit growth ceases at air temperatures below about 10°C and very high air temperatures – certainly above 35°C – can also retard growth (Malézieux *et al.*, 1994). The effect of cold is especially pronounced. In winter in cool subtropical regions, such as southern Queensland, Australia, forcing of 'Smooth Cayenne' initiates reproductive development even though temperatures are too cold to allow for significant fruit development. The delay in development collapses the harvest dates of plants forced up to 13 weeks apart into a period of no more than 3 weeks (Sinclair, 1992a). Thus, on average, fruit from plants forced on about 1 June are harvested on 2 March, a fruit development period of 274 days, while fruit from plants forced on about 1 September are harvested on 24 March, a fruit development period of only 204 days.

Inflorescence and Fruit Morphology and Growth

Early development

The meristematic area of the pineapple stem is small relative to the diameter of the stem near its apex. The vegetative apical dome is very small, but it broadens considerably after inflorescence induction has occurred. At the onset of reproductive development, leaf primordia width decreases and the number of primordia bordering the dome increases considerably (Kerns *et al.*, 1936; Bartholomew, 1977; compare Fig. 8.1A and B). At this early stage, the first structures of the inflorescence to develop are bracts, and

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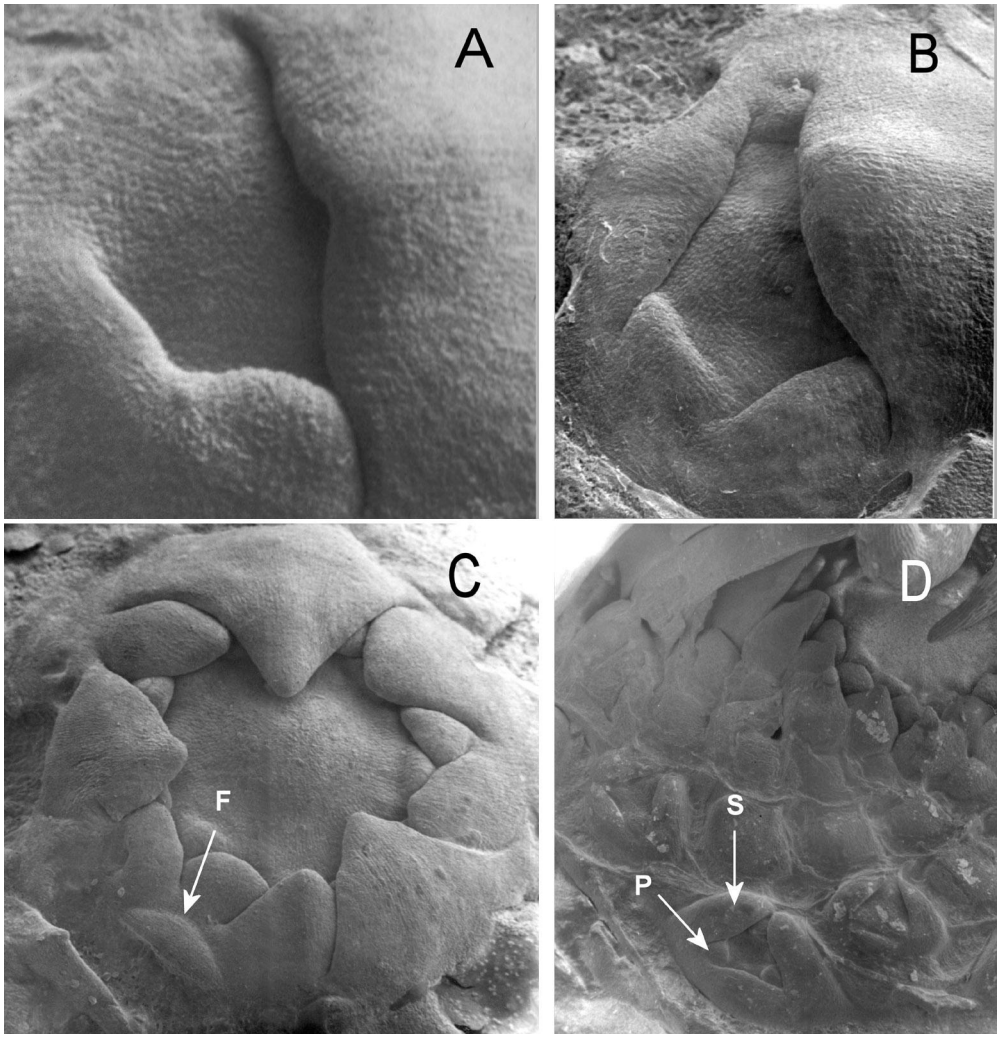

Fig. 8.1. Scanning electron photomicrographs of stem apical development of 'Smooth Cayenne' pineapple after forced induction of inflorescence development with ethephon. A, Vegetative apex at approximately 185× showing two leaf primordia surrounding the apical dome. B, Apex at approximately 133× 8 days after induction showing additional primordia surrounding the apical dome as a result of induction. C, Apex at approximately 84× 11 days after induction, showing increasing numbers of primordia. The bract at the lower left of the photograph has been removed to show the first floret primordium (F). D, Apex at approximately 40×, with floret bract primordium removed to show the developing sepal (S) and petal (P) primordia. (From Bartholomew, 1977.)

each fruitlet forms in the axil of these bracts (Fig. 8.1C). Shortly after the bracts have been initiated, three sepal and petal primordia can be seen developing (Fig. 8.1D) and, soon-thereafter, six stamen primordia develop. The flower parts all originate at the same level and grow away from their point of origin. As they grow upward, a cavity is formed, which eventually closes over and three carpels are formed within it. The apex of the vegetative plant stem is broad and flat, but, as the first flower structures begin to develop, the stem apex narrows and the fruit stem or peduncle begins to elongate (Fig. 8.2).

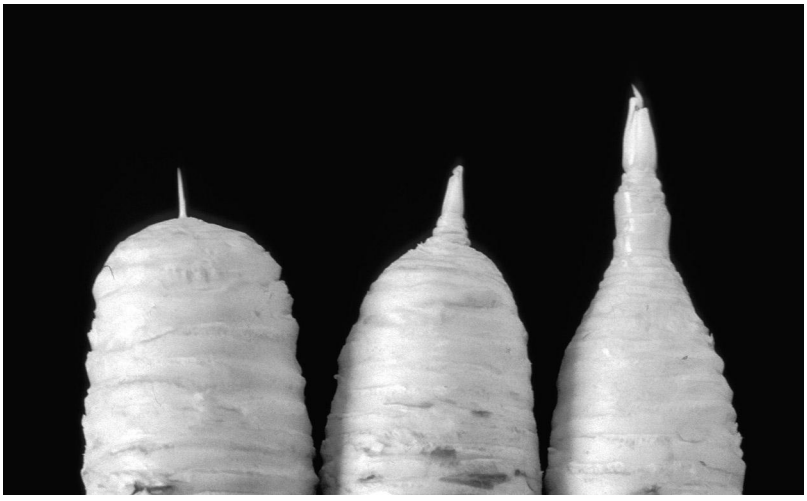

Fig. 8.2. Vegetative (left) and reproductive stems of 'Smooth Cayenne' plants after induction with ethephon. Note the progressive elongation of both the upper portion of the stem and the fruit stem (peduncle).

The elongation of the stem tip in a cross-section taken through the centre of the plant is diagnostic of natural or growth-regulator-induced inflorescence development and can usually be seen within 2 weeks after induction has occurred. Development of the florets at the base of the young inflorescence continues at the same time that new bract and flower primordia are being produced higher on the young inflorescence (Fig. 8.3A). Eventually all flower parts become enclosed by the developing sepal primordia and are no longer visible without dissection (Fig. 8.3B). The number of florets that develop on a fruit varies considerably with the variety of pineapple, the size of the plant at induction, plant population density, the quality of forcing and other factors that have not been adequately characterized. For 'Smooth Cayenne' pineapple, at between 30 and 40 days after induction, the diameter of the apical dome decreases, the initiation of reproductive structures ceases and leaf bracts (Fig. 8.4) and, later, crown leaves begin to develop (Kerns *et al.*, 1936; Bartholomew, 1977). By the time crown leaves are visible, there has been considerable elongation of the peduncle and the leaves (bracts) in the centre of the leaf whorl have turned red to red-orange.

The rate of early development of the 'Smooth Cayenne' inflorescence and fruit is determined almost entirely by the prevailing temperature of the environment where the crop is grown (Fleisch and Bartholomew, 1987; Malézieux *et al.*, 1994). In the warm subtropical environment of Hawaii, fruitlet initiation ceased about 34 days after forcing with ethephon in midsummer (Bartholomew, 1977) and after 37 days in December (Kerns *et al.*, 1936). In the somewhat warmer Côte d'Ivoire, when plant leaves were removed every few days after forcing, fruitlet number was reduced up to the 30th day after forcing (E. Malézieux, 1992, unpublished results), indicating that fruitlet number was fixed by 30 days after forcing in that environment. Beyond that time, leaf removal had no effect on fruitlet numbers. Cell division continues in the fruit until after anthesis and further development thereafter is primarily the result of cell enlargement (Okimoto, 1948).

The stages of fruit development after induction that can be defined on the basis of developmental morphology include the beginning and end of floret (fruitlet) initiation, the beginning and end of anthesis (flowering) and maturation. Other 'stages' have been defined for convenience in estimating progress towards maturation or to

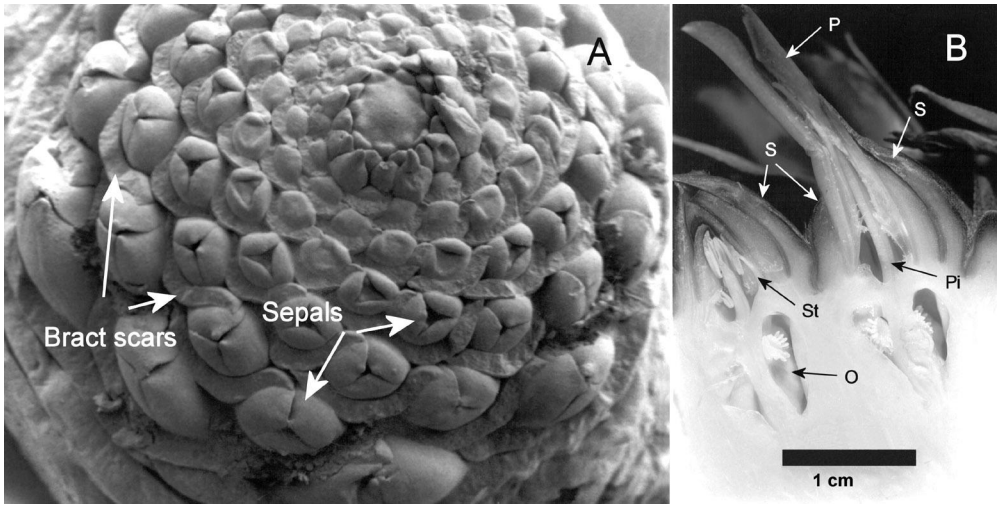

Fig. 8.3. A, Young developing pineapple inflorescence (20×) with the bracts subtending the florets removed (bract scars) at 25 days after induction in the summer in Hawaii (from Bartholomew, 1977. © The University of Chicago, all rights reserved). B, Section through two 'Smooth Cayenne' florets at anthesis; S, sepals; P, petals; St, stamen; Pi, pistil; O, locule of ovary with ovules.

Fig. 8.4. Stem apex (138×) at 47 days after induction in the summer in Hawaii. Note the small apical dome with a reduced number of primordia surrounding it when compared with Fig. 8.3A. (From Bartholomew, 1977. © The University of Chicago, all rights reserved.)

help in determining when disease organisms might enter the fruit (Rohrbach and Taniguchi, 1984). The earliest stage that can be seen in the centre of the leaf whorl as the peduncle elongates without sacrificing the plant is commonly referred to as 'open heart' and the width of the opening is commonly estimated for crop-logging purposes. At the time the 'open heart' stage is reached, inflorescence bracts have turned bright red to red-orange.

The extent of open heart is defined by the diameter of the opening – nominally 1.0 or 2.0 cm (½ and 1 in. are used in Hawaii) (see Fig. 9.30) – and days from forcing to one of the open-heart stages is a valuable criterion for assessing the quality and effectiveness of forcing. These 'stages' are more quantitative than the sometimes used red-bud stage, which is less sharply defined.

The developing inflorescence is typically completely visible within 7–10 days after the 2.0 cm open-heart stage has been reached, and this has been referred to as the 'early cone' stage (Rohrbach and Taniguchi, 1984). By this stage, the sepals and bracts of the fruit floret are visible and the number of fruit florets can be counted. The stages 'mid-cone' and 'late cone' follow at approximately weekly intervals in summer in Hawaii and anthesis begins approximately 1 week after late cone. The tip of the corolla, typically blue, can usually be seen by the late-cone stage. Anthesis, which occurs progressively from the base upward, usually takes from 15

to 25 days, depending on the floret number and the average temperature. As is typical of the growth of most structures, the increase in fruit fresh and dry weight from the time of induction to maturity is sigmoid (Sideris and Krauss, 1938). Growth rate, discussed in more detail later, is primarily dependent on temperature.

Fruit growth and ripening

The time from induction to maturity is a characteristic of the clone or variety and is greater for 'Smooth Cayenne' and 'Pernambuco' than for the 'Spanish' and 'Queen' varieties (Py *et al.*, 1987). However, Chan and Lee (2000) found little difference in the time from induction to harvest among F1 progenies. Earliness was associated primarily with the time required to reach a plant weight suitable for induction.

Growth in fruit weight, and presumably volume, is sigmoid (Sideris and Krauss, 1938), with the main biochemical changes associated with maturation, such as accumulation of sugars and carotenoids, occurring in the last weeks of development (Gortner *et al.*, 1967; see Paull and Chen, Chapter 10, this volume). With 'Smooth Cayenne', the external signs of approaching maturity are the flattening and increased gloss of the surface of individual fruitlets. As with anthesis, fruitlet maturation occurs progressively from the base to the top of the fruit. As ripening occurs in 'Smooth Cayenne', the fruitlet epidermis typically turns yellow progressively from the base to the top, though, in some locations or at some times of the year, the shell does not colour as the fruit matures and green-shell ripe fruit are produced. Large fruit weighing 2.0 kg or more will have basal fruitlets that are overmature by the time the upper fruitlets ripen so overall fruit quality is near optimum when large fruits are about half yellow. The fruit does not show a respiratory climacteric during ripening, perhaps because it is an aggregate of many fruitlets, all at different stages of development. Aspects of the physiology of fruit development are discussed later in the chapter.

Factors Affecting Induction of Inflorescence Development

The success of forcing is related to plant sensitivity to induction, i.e. the probability of the occurrence of natural induction. The higher the plant sensitivity, the more likely that forcing will be successful. Success is measured by the fact of induction (percentage of plants induced), the quality of the induction (fruitlets initiated per unit of plant weight) and the sharpness of the harvesting peak. Fruitlet numbers per fruit is established at induction and, thereafter, fruit growth and enlargement become the determinants of yield. Fruit growth and enlargement are optimum when conditions for plant growth are optimum. These topics are covered in other chapters in the book. Maturation of fruits within a field has a natural spread over time and, where forcing is poor, fruit mature over a wider time span than where forcing is good. The sharpness of the harvesting peak affects the number of fruits actually recovered from the field and the cost of harvesting.

In the following sections, the processes of natural and forced induction, inflorescence development and yield elaboration are reviewed. Lastly, those preharvest factors that affect postharvest quality are reviewed.

Natural induction of flowering

'Smooth Cayenne' pineapple must attain some minimum plant weight before natural induction of inflorescence development can occur (Py *et al.*, 1987). The minimum weight has not been well characterized but probably exceeds 1.0 kg in most environments and is greater in warm than in cool environments. Collins (1960) considered 'Smooth Cayenne' to be a perennial that would continue to grow as long as environmental conditions were adequate. There are, however, few regions where environmental conditions are constantly optimum for growth. Seasonal patterns in natural flower initiation are, therefore, evident in most regions. These patterns have long been recognized and were the basis for commercial pineapple

production before the discovery of chemical flowering agents.

Once the minimum plant weight is reached, the factors that promote flowering are mainly those that retard vegetative growth. For 'Smooth Cayenne' grown in subtropical regions, there is a strong wave of natural induction in the autumn-winter season. Natural flower initiation can, however, occur at other times of the year (Millar-Watt, 1981; Sinclair, 1997, 1998, 1999), so those plants that do not flower naturally in the winter may flower in midsummer.

Definite peaks in natural initiation are also recognized in tropical regions (Aubert, 1977; Wee, 1978; Giacomelli *et al.*, 1984). The main peak usually occurs when either minimum or maximum temperatures are at their lowest. This peak is also associated with a decline in the hours of solar radiation. A small peak also occurs when maximum temperatures are at their highest (Teisson, 1972). Gowing (1961) indicated that, depending on the kind of planting material used and the time of planting, natural initiation could occur in any month of the year in Hawaii (latitude 21°N).

Inhibition of natural induction is associated with those factors that promote vegetative growth. For example, vigorous growth, stimulated by excessive nitrogen and warm night temperatures, inhibits flowering (Nightingale, 1942; Bartholomew and Kadzimin, 1977; Conway, 1977).

Photoperiod

The earliest work on photoperiod by Van Overbeek (1946) showed that pineapple responded like a short-day plant. The work of Gowing (1961) later established that 'Smooth Cayenne' was a quantitative short-day plant, i.e. flowering can occur at any day length but is accelerated by short days (Taiz and Zeiger, 1991). Gowing (1961) observed that flowering of 'Smooth Cayenne' was not inhibited by day lengths in excess of 13 h. He also found that interruption of the dark period suppressed flower initiation, so it was concluded that long nights favoured induction. A subsequent study by Friend and Lydon (1979) showed that, for 'Smooth Cayenne', 8 h days were more inductive than days of 10, 12 or 16 h.

Solar radiation

There is little evidence to indicate that solar radiation *per se* has any direct role in natural flower induction. It seems most likely that natural induction in regions away from the equator is explained by a combination of short photoperiods and cool temperatures. However, natural induction also occurs in equatorial regions, where photoperiod is almost constant and temperatures are generally higher. In equatorial regions such as Côte d'Ivoire, West Africa (latitude 5–10°N), and tropical western Malaysia (latitude 1°17'N), the periods of greatest natural flowering coincided with decreases in maximum (Teisson, 1972) or minimum temperature (Wee, 1978). In Malaysia there was also a correlation with a decrease in hours of sunshine (Wee, 1978). Bourke (1976) found no correlation between sunshine hours and natural flower induction in 'Queen' pineapples in Papua New Guinea (latitude 4°21'S) once the variance associated with low temperature was removed.

Temperature

While 'Smooth Cayenne' pineapple is considered a short-day plant, cool temperatures in particular enhance the flowering response. It is worth remembering that the optimum temperatures for growth of pineapple are considered to be close to 30°C day and 20°C night with an optimum mean of about 24°C (Neild and Boshell, 1976; Bartholomew and Malézieux, 1994).

Van Overbeek and Cruzado (1948b) established that a night temperature of approximately 16°C over 30 days induced flowering in 88% of 'Red Spanish' plants during late summer in Puerto Rico; 28% of plants held at a night minimum temperature of 22°C also flowered. A night minimum temperature of 16°C was therefore more inducive than 22°C for 'Red Spanish'; the optimum temperature for flowering is not known.

Gowing (1961), using 'Smooth Cayenne', compared night temperatures of 15, 23 and 26°C and found that a night temperature of 15°C induced flowering when in combination with a short day length for a period of

30 days. At normal day lengths (*c*. 12.5 h) this same low night temperature over 30 days did not induce flowering. However, exposure to a constant 18°C for 9 weeks was claimed to be more effective. The longer period of exposure was probably the main factor accounting for the improved response. A more recent study by Sanewski *et al*. (1998) supports this observation. Sanewski *et al*. (1998) found that a constant 20°C for 10 weeks induced flowering in 100% of 'Smooth Cayenne' plants but a constant 10 or 15°C for up to 12 weeks did not induce flowering. These studies were conducted during a time when day length decreased from 12.5 to 10.5 h and natural induction was most prevalent in the field. A subsequent study (G. M. Sanewski, 1999, unpublished results) confirmed that a constant 20°C was more effective than 20/15°C or 25/15°C for up to 64 days. A day/night combination of 25/20°C was as effective as a constant 20°C over 64 days. This suggests that, for 'Smooth Cayenne' at least, night temperatures below 20°C are not as effective as 20°C, and a day temperature of 25°C is as effective as 20°C when in combination with a 20°C night.

Friend and Lydon (1979) also found that, with a photoperiod of 8 h and day temperatures of 25 or 30°C, a night temperature of 20°C was more inductive for 'Smooth Cayenne' than night temperatures of 15, 25 or 30°C. Flowering was induced at night temperatures of 15 and 25°C but not at 30°C. In a review of natural flower initiation of 'Queen' pineapple in Papua New Guinea, Bourke (1976) concluded that natural induction was closely associated with minimum temperatures of 20–23°C. It appears, therefore, that exposure to temperatures of as high as 25°C for at least the nocturnal period, in combination with a short day length will induce flowering in 'Smooth Cayenne' if these plants are exposed to these conditions for 9–10 weeks. A night temperature of 20°C in combination with a day temperature of 20–25°C is believed to be close to optimal.

Nightingale (1942) suggested that sudden brief periods of very low temperature (*c*. 5–10°C) can induce flowering. Yow (1959) indicated that 5°C for 2–3 days was correlated with flower induction of 'Smooth Cayenne' in Taiwan. While there are few data on the effects of a sudden drop in temperature on natural induction, it is possible that the sudden interruption in growth might induce flowering in a small percentage of plants if other conditions are also favourable.

The effect of temperature perturbations can, however, be difficult to interpret. Though conclusive data are lacking, it is also possible that, in addition to the effect of cool temperature, diurnal warming during winter may also increase the incidence of natural induction. In a comparison of six planting densities in subtropical Queensland, Scott (1992) found that the incidence of natural flowering of the ratoon crop increased consistently from 3.5 to almost 12% as plants ha^{-1} decreased from 80,695 to 46,112. No leaf- or plant-weight data were taken for the ratoon crop, so it is not possible to rule out differences in plant weight as a factor in this study. Further evidence of an effect of diurnal warming on flower induction is the common observation in subtropical Queensland that natural flowering is more prevalent in outside rows, where incident radiation and diurnal plant temperatures are expected to be greater. There is, however, the possibility that the increased natural initiation is a direct response to increased light interception and not the subsequent rise in plant temperature. While this is possible, data collected by Sanewski *et al*. (1998) suggest that warming after exposure to cool temperatures has a direct positive effect on natural initiation. In their study they collected mature suckers of 'Smooth Cayenne' from the field in late winter and placed them at either 5, 10 or 28°C for 3 days. Exposure of plants to 28°C induced flowering in 75% of plants. There is clearly a need for further study of the effects of temperature and its interaction with solar radiation on plant sensitivity to natural and forced induction.

In addition to the effects of low temperature, it is also commonly recognized that natural induction will occur after brief periods of high temperature. In Australia, these events have been associated with diurnal maxima of 40°C over 2 days (Sinclair, 1997) and is probably the result of wound-

induced ethylene production. There is good circumstantial evidence that ethylene is involved in the flower-induction process. Environmentally induced flowering is assumed to result from increased production of ethylene or heightened plant sensitivity to ethylene, or both.

Recent studies (Botella *et al.*, 2000; J. Botella, 1999, personal communication) indicated that there is more than one gene in pineapple leaf tissues that codes for the production of ACC synthase, the enzyme that produces 1-aminocyclopropane-1-carboxylic acid (ACC), the precursor of ethylene. One gene codes for an ACC synthase that is regulated by cool and warm temperature and this enzyme is identical to the one regulated by auxin application. Apparently a different gene is involved in the production of the ACC synthase produced as a result of wounding of leaf tissues. It seems likely that temperature induces flowering by affecting different ethylene pathways. Temperature, depending on its degree and duration, could stimulate natural ethylene production and thus induce flowering by affecting both the auxin- and wound-induced pathways.

Water availability

Water stress and water excess are often implicated in a flowering response in tropical and subtropical species. An increase in ethylene production is often associated with water stress in plants (Yang and Hoffman, 1984), but there are conflicting reports on this point. For example, Morgan *et al.* (1990) found only slight, transient ethylene production on rewatering cotton subjected to water deficit but no response in beans or roses. Nevertheless, it is generally believed that pineapple flowering may be induced in response to a seasonal water deficit and induction also occurs in response to water excess (Py, 1964), due to growth inhibition or enhanced ethylene production, or possibly both. Tay (1974) reported that both water excess and water deficit delayed natural induction of pineapple grown in peat soil, while growth and natural induction were enhanced by increasing watering frequency. Consistent with the results of Tay (1974), Min (1995) found that a severe water deficit decreased the plant's susceptibility to ethephon and did not induce natural flower initiation. Mild water deficit was not studied. Water excess increased ethylene production of the basal white tissue of 'D' leaves by approximately 100% but did not induce flowering. The fact that excess water increased ethylene production so substantially suggested it should increase the plant's susceptibility to flowering and may therefore be implicated in some situations. Waterlogging, a more severe degree of water excess, had no effect on ethylene production or flowering (Min, 1995).

Much of the inconsistency in the effect of plant water status on flower initiation is probably due to differences in the severity of deficit or excess imposed. Severe and sudden deficit or excess are likely to result in a cessation of all enzymatic processes, including those involved in flower initiation.

Genetic variation

Most pineapple genotypes appear to be more susceptible to natural flower initiation than 'Smooth Cayenne'. The natural flowering cycle in wild types, such as *Ananas ananassoides* and *Ananas parguazensis*, is usually annual (Leal and Coppens d'Eeckenbrugge, 1996). In an *Ananas* spp. germplasm collection held in subtropical Australia (latitude 27°S), plants of 'Pernambuco' and 'Mordilona Queen' and the species *A. ananassoides* all flower naturally more frequently than does 'Smooth Cayenne'. Williams (1987) reported that some hybrids flower when they reach a plant weight of about 1.5 kg, regardless of the time of year.

Van Overbeek and Cruzado (1948b) reported that 'Red Spanish' was less responsive to day length than 'Cabezona', but more responsive to low temperature. 'Cabezona' is a triploid cultivar of the 'Spanish' type (Samuels, 1969). In Malaysia, 'Smooth Cayenne' is considered to be a vigorous plant that it is more difficult to force than is 'Singapore Spanish' (Dunsmore, 1957), the main canning variety there.

It is assumed that the relatively low incidence of natural flowering in 'Smooth

Cayenne' and the associated ease of crop control in comparison with other types of pineapple account to a substantial degree for its popularity and may be the most important factor allowing large-scale production of this variety.

Geotropic stimulation

Van Overbeek and Cruzado (1948a) reported that plants of 'Cabezona' pineapple could be geotropically stimulated to flower, as indicated by a strong flowering response when plants were held horizontally for 3 days or more. It was theorized that flowering was induced by the accumulation of endogenous auxin in the lower longitudinal half of the stem apex, though Salisbury and Ross (1992) note that many gravitropic responses can be attributed to increased sensitivity to auxin rather than an increase in concentration.

In summary, both environmental and cultural factors can contribute to natural induction in 'Smooth Cayenne' pineapple. 'Smooth Cayenne' shows a clear response to day length and temperature and probably a weaker response to solar radiation. Surprisingly, very low temperatures are not commonly implicated in the incidence of natural induction. Flowering is more likely to occur as a result of moderate (around 20°C) temperatures, not much lower than the optimum for growth, sustained over many weeks in combination with a short day length. Ethylene production resulting from mild to moderate wounding of plant tissues due to sudden exposure to short periods of very high or very low temperatures appears a minor cause. Plant water status is probably also implicated in a minor way, though supporting data are lacking.

Forced induction of flowering

Late in the 19th century it was discovered that pineapple inflorescence development could be forced with smoke (Collins, 1960) and later research showed that the active ingredient in smoke was ethylene (Rodriquez, 1932). Work in Hawaii (Collins, 1960) showed that acetylene gas could also force inflorescence development of pineapple and that water-saturated solutions of acetylene or ethylene sprayed over plants could deliver the required quantity of either gas. Green leaf tissue is required for forcing with ethylene (Traub *et al*., 1940), probably because the principal point of entry for gases is through the stomata. Calcium carbide, which releases acetylene on contact with water, also forces flowering. Calcium carbide must be placed in the centre of each plant, which precludes mechanization.

Later work showed that a variety of synthetic auxins also forced flower development of 'Smooth Cayenne' pineapple (Collins, 1960). The auxin used commercially was the sodium salt of naphthalene acetic acid (NAA) (Collins, 1960; Bartholomew and Criley, 1983). Almost 20 years after the commercial use of NAA began, Burg and Burg (1966) showed that auxins applied to pineapple stimulated natural ethylene production and speculated that the ethylene actually forced flower development.

Shortcomings with auxins and the technical and managerial difficulties associated with the use of acetylene and ethylene led to a continued search for better forcing agents. Over 700 compounds were screened during the 1950s but none were found to be better than NAA, acetylene or ethylene (Gowing and Leeper, 1959). At about the same time, Gowing and Leeper (1955) reported that β-hydroxyethylhydrazine (BOH) could force pineapple to flower. Palmer *et al*. (1967) showed that BOH decomposed to produce ethylene. It seems likely that the ethylene released from BOH induced flower development and the fact that BOH was most effective when applied at night is strong evidence for this.

Ethephon, which degrades to produce ethylene and may also stimulate ethylene production by the plant, was identified in the 1960s (Cooke and Randall, 1968). Extensive research (Bartholomew and Criley, 1983; Py *et al*., 1987) has demonstrated the efficacy of ethephon as a forcing agent in a wide range of environments where pineapple is grown. While ethephon is less effective than ethylene in the warm tropics, its

ease of use has caused it to be widely adopted for flowering of pineapple.

The almost universal induction of flowering with a growth regulator is almost unique to pineapple. Where the climate is favourable, the commercial exploitation of this response (see Hepton, Chapter 6, this volume) makes it possible to produce fruit in all months of the year. Year-round forcing and harvesting of pineapple make efficient use of available labour and provide a steady supply of pineapple to the cannery and the fresh-fruit market. Forced induction reduces variability in time of fruit maturation within a field, such that most of the fruits can be harvested within a few weeks. This period can be shortened by application of ethephon to mature green fruits to enhance fruit shell colour (see Hepton, Chapter 6, this volume). While pineapple is generally easy to force, plant sensitivity to forcing varies considerably. It is important to understand how plant sensitivity varies, because such knowledge can help increase forcing success.

Plant sensitivity to forcing

Variation in plant sensitivity to forcing in different months of the year has been documented for 'Singapore Spanish' (Wee and Ng, 1968; Wee and Rao, 1977) and 'Smooth Cayenne' (Py *et al*., 1987), and it is likely that other varieties also show such variation. As with natural induction, plants smaller than some minimum weight – usually somewhat less than about 1.0 kg fresh weight in subtropical regions – are not easily forced. However, forcing of plants of small weight is of little consequence to commercial growers because plants too small to be forced will not produce fruit of marketable size. Once a minimum plant size has been attained, plant sensitivity shows little variation with increasing weight to some upper limit. Above this upper limit, which has not been well characterized, 'overly large' plants are reported to be more difficult to force than those considered to be of optimum size (Bartholomew and Criley, 1983; Py *et al*., 1987). The cause of this reduced sensitivity is not known, but it may be related to a rapid growth rate, intense mutual shading or difficulty in delivering a growth regulator to susceptible tissues, or to more than one factor. As with very small plants, the issue is a minor one because growers would normally force induction before sensitivity begins to decline.

For plants of sufficient size, sensitivity to forcing reaches a maximum during the time of year when natural induction normally occurs. Outside this time, the sensitivity to forcing is determined primarily by the prevailing temperature, and this is true for both 'Singapore Spanish' and 'Smooth Cayenne' pineapple (Wee and Rao, 1977; Bartholomew and Malézieux, 1994). In warm tropical regions, sensitivity to forcing, even during the time of natural induction, tends to be low because growing conditions are optimum and growth is rapid. For 'Smooth Cayenne', sensitivity usually decreases with increasing night temperature above about 25°C. In such environments, special care must be taken in order to ensure that a high percentage of plants in a field are forced. However, if vigorously growing plants can be forced, fruitlet numbers are high and, if conditions for fruit filling are favourable, large fruit are produced at harvest.

Outside the season when natural induction normally occurs, and particularly during the warmer months of summer, a reduced sensitivity to forcing that is short-term in nature is observed. This sensitivity is associated with the short-term effect of high day temperatures, usually above 32°C on a given day, although night temperatures may also be high. This type of reduced sensitivity, which is often seen during January and February in southern Queensland, determines not only whether plants can be forced, but also the 'quality' of the force (Wassman, 1991). 'Quality' of forcing is a subjective term used to characterize the intensity of the plant response to the plant-growth regulator as reflected in the time from forcing to the appearance of the inflorescence in the plant heart and the number of fruitlets initiated by plants of comparable size within a given environment. When the quality of the force is poor, fewer fruitlets per fruit will be initiated, fruit emergence is delayed and fruit weight and yield are markedly reduced

(Wassman, 1991). However, if the following day is cooler, sensitivity may be high and forcing is easily accomplished (Wassman, 1991). No data were found regarding what step in the induction process, i.e. fruitlet initiation or fruit development, is delayed on hot days when forcing is poor.

Variation among genotypes

As with natural induction, comparative studies show that clones of 'Smooth Cayenne' are less easily forced than are other varieties of pineapple (Wee and Ng, 1970; Py *et al.*, 1987). In Malaysia, 'Singapore Spanish' was the dominant canning variety for many years, mainly because it could be forced in this tropical region in all months of the year. 'Smooth Cayenne' pineapple grown on the peat soils of Malaysia is difficult to force in most months of the year. Breeding to improve plant and fruit characteristics has resulted in intervarietal hybrids of 'Smooth Cayenne' that are easier to force than 'Smooth Cayenne' and have higher yield and better flesh colour than 'Singapore Spanish' (Chan and Lee, 1985; Chan, 1986). G.M. Sanewski (1999, personal observation) also found that intervarietal hybrids are more readily induced to flower than is 'Smooth Cayenne'.

Environment

The environmental factors that promote natural induction also increase sensitivity to forcing. Variation in plant sensitivity has been detected when plants were forced with acetylene, NAA or ethephon, presumably because these plant-growth regulators have been widely used in a variety of environments. The relative effectiveness of acetylene, ethephon and NAA in forcing flowering varies and this variation is discussed below.

During the time of natural induction, there is little need for concern about the efficacy of the growth regulator. Induction of flowering outside this season can provide a severe test of forcing practices, especially for 'Smooth Cayenne'. Sensitivity to forcing is enhanced by short days, cool temperatures and, where plants are likely to have reduced sensitivity, moderate nitrogen stress, established by withholding nitrogen fertilizer for 4–8 weeks prior to forcing. When forcing with NAA, the nitrogen content of the 'D' leaf should not exceed 1.6% and a level of 1.3% is recommended, especially if plants are expected to be difficult to force (Py *et al.*, 1957).

The effect of moderate water stress is apparently similar to that of moderate nitrogen stress (Evans, 1959), but no controlled studies were found. Severe water stress causes plants to be unresponsive to forcing (D.F. Williams, 1985, personal communication), presumably because severe water stress probably causes all developmental processes to cease, thus rendering the plant insensitive to growth regulators.

When weather–shelter temperatures in subtropical regions exceed 28°C (Glennie, 1979) or 32°C (Wassman, 1991) during the day, forcing with ethephon is difficult. Under such conditions, leaf temperature may be 20°C higher than air temperature (Bartholomew and Malézieux, 1994) and high leaf temperatures reduce leaf carbon-assimilation rates (Zhu *et al.*, 1999). In tropical countries, such as Côte d'Ivoire, Malaysia and Thailand, which have high average night temperatures, 'Smooth Cayenne' is difficult to force with ethephon and even more so with NAA (Py *et al.*, 1987). Average night temperatures of 25°C or greater can reduce the percentage of plants forced (Conway, 1977) and the size of the fruit (Min and Bartholomew, 1997). Night temperatures of 25 and 30°C reduce natural ethylene production, CO_2 fixation at night into malic acid (Min and Bartholomew, 1997), total carbon assimilation (Zhu, 1996) and fruitlet number (Min and Bartholomew, 1997) of plants forced with ethephon. It seems likely that any environmental factor that reduces net assimilation, either by reducing photosynthesis or increasing respiration, at the time of forcing will reduce fruitlet number and thus fruit weight at harvest.

Other factors affect the number of florets initiated on a plant of a given weight, but for the most part these appear to be unrelated to variations in plant sensitivity to forcing. These

effects are discussed under Inflorescence and Fruit Development and Yield below.

Effectiveness of plant growth regulators

There is considerable variation in the effectiveness of the plant-growth regulators that have been widely used to force induction (Bartholomew and Criley, 1983). This information is summarized below, with the discussion limited to those plant-growth regulators that have been extensively studied.

ETHYLENE, ACETYLENE AND CALCIUM CARBIDE. The discussion of these three agents is combined here because pineapple responds to acetylene as it does to ethylene, and calcium carbide releases acetylene when it comes into contact with water. Ethylene properly applied with a pressurized sprayer late in the evening or at night to permit uptake through the stomata when they are open (see Malézieux *et al*., Chapter 5, this volume) is a highly effective forcing agent, though comparative studies show little difference between ethylene and acetylene. In Queensland, ethylene was used as a saturated solution in 6500–9000 l ha^{-1} of water or two applications of 4500 l ha^{-1} were applied 24 h apart. Py *et al*. (1987) state that 800 g of ethylene is applied in 6000–8000 l of water ha^{-1}. Activated charcoal at 20 g l^{-1} was added to the water to increase absorption of the ethylene in the solution. Plants forced with ethylene produce fruits with physical dimensions similar to those produced by natural induction. Special equipment is required to prepare the solution for application, as the gas is highly combustible.

The physiological response to acetylene mimics that of ethylene. Acetylene is more commonly used on small farms because a saturated solution can be made in a pressurized hand or backpack sprayer, using cold or iced water and calcium carbide. Acetylene (Gowing and Leeper, 1959; Yow, 1972) and ethylene (Py *et al*., 1987) were uniformly effective in forcing pineapple when applied at night but unreliable when applied during the day, except on cool, cloudy days (Yow, 1972) or late in the evening. A comparative study showed acetylene to be as effective as ethylene, while being cheaper and more convenient to use (Lewcock, 1937). Usually 10–50 ml of solution is applied to each plant (Py, 1953; Py *et al*., 1987) in the late evening or at night with a pressurized sprayer.

Calcium carbide, which produces acetylene on contact with water, is a highly effective forcing agent, though apparently not as effective as acetylene. The effectiveness of calcium carbide, relative to acetylene, is probably related to the timing and speed of release of acetylene. Consistent with the assumption that acetylene and ethylene move into the plant through the stomata, calcium carbide was more effective if applied at night rather than during the day (Aldrich and Nakasone, 1975). Approximately 1.0 g of calcium carbide is applied by hand into the centre of each plant (Py *et al*., 1987). If no water is present in the centre of the plant, water may be poured into the plant to release acetylene. Hand application limits the use of calcium carbide to small farms.

NAPHTHALENE ACETIC ACID. Prior to the discovery of ethephon, the sodium salt of NAA, commonly referred to as SNA in Hawaii, was widely used to force pineapple into flower. Typically, about 50 g of NAA was applied in 900–1000 l ha^{-1} of water. While NAA is easy and inexpensive to use, it is less effective than ethylene, acetylene or ethephon, particularly in warm tropical environments. In regions having high average temperatures, NAA may only be effective up to 2 months prior to the time when natural initiation would be expected (Py *et al*., 1987) and earlier application may be ineffective. Under less than ideal conditions, double applications spaced about a week apart are essential to force a high percentage of plants. Relative to plants forced with acetylene, ethylene, BOH and ethephon, maturation of fruit of plants forced with NAA is delayed by 1–2 weeks (Yamane and Ito, 1969). It has been speculated that NAA forcing is due to the production of ethylene (Burg and Burg, 1966) and peak ethylene production by plants treated with NAA occurs a few to several days after the treatment. For the above reasons and because plants forced with NAA

produce a slightly smaller, more elongated fruit with a somewhat tapered top (Leeper, 1965; Yamane and Ito, 1969), a less-than-ideal shape for canning, ethephon has largely replaced NAA as the forcing chemical of choice. NAA is no longer registered for use in the USA.

β-HYDROXYETHYLHYDRAZINE (BOH). Plants forced with BOH produce fruit comparable in weight and shape to fruit from plants forced with ethephon. Harvest date in most cases was also similar to that for plants forced with ethephon and, at some times of the year, 6–10 days earlier than plants forced with NAA (Leeper, 1965; Yamane and Ito, 1969). Usually 3.0 kg of BOH in 1135 l of water (Yamane and Ito, 1969) or 2000 l ha^{-1} of a 2500 p.p.m. active ingredient (a.i.) solution was applied (Py *et al.*, 1987). For best results, BOH was applied late in the evening or at night. Because BOH degrades to produce ethylene (Palmer *et al.*, 1967), it is assumed that this ethylene actually forces flower development. Higher concentrations of BOH are phytotoxic, with symptoms developing soon after application (Anon., 1975). BOH is not registered for use in the USA because the chemical was identified as a potential carcinogen.

ETHEPHON. Ethephon is less effective in forcing pineapple than are ethylene and acetylene but is ideal in environments where plant sensitivity to forcing is relatively high. An important advantage of ethephon under conditions ideal for forcing is that it can be applied with a boom sprayer during the day or night with equal effectiveness. Ethephon is typically applied in a 2–5% (weight : volume) urea solution. Nitrogen sources such as ammonium nitrate and ammonium sulphate do not provide the same enhancement of ethephon activity as is provided by urea (Yamane and Ito, 1970). The mechanism by which urea enhances the activity of ethephon is not known. Studies with radiolabelled ethephon show that urea does not increase absorption (Turnbull *et al.*, 1993, 1999). High solution pH hastens the rate of ethephon breakdown to ethylene, but urea only slightly increases solution pH. The addition of 2.9 l of ethephon (39.5% a.i.) to 1794 l of 2.7% urea–water solution raised the pH from 2.90 to 3.20 (Yamane and Ito, 1970). Glennie (1979) reported that a solution containing 480 mg l^{-1} of ethephon had a pH of 2.7, while adding 5% urea increased the solution pH to 3.0 and, at that pH, the solution half-life was 75,000 h.

Forcing with ethephon is more difficult when day temperatures are > 28°C (Glennie, 1979) or > 32°C (Wassman, 1991) and in tropical regions with high average temperatures. There are two approaches to improving the effectiveness of ethephon. In the first, the amounts of ethephon applied can be increased. Under ideal conditions, 0.5 kg ethephon a.i. is applied in 2000–3000 l ha^{-1} of a urea–water solution (Bartholomew and Criley, 1983; Py *et al.*, 1987). When leaf nitrogen is high, up to 6 kg ha^{-1} may be required (Guyot and Py, 1970). Higher amounts have been reported to reduce fruit weight (Dalldorf, 1979; Iglesias, 1979); however, others (Yamane and Ito, 1969; Guyot and Py, 1970) found no reduction in fruit weight or length, or other evidence of phytotoxicity when more than 16 kg ha^{-1} was applied. However, Yamane and Ito (1969) found that slice recovery declined significantly at 13.4 and 17.9 kg ethephon ha^{-1} and sucker numbers declined significantly when 9 kg ha^{-1} or more was applied.

The second way of improving the effectiveness of ethephon is to raise its pH, which, as discussed above, increases its rate of breakdown to ethylene. Cox (1979) showed that the half-life of ethephon at 25°C is 761 h at pH 5, but drops to 12 h at pH 9. Glennie (1979) showed that, at this temperature at pH 3, the half-life was 75,000 h. At pH 9.2 at the temperatures experienced in Australian fields, ethylene release is rapid, and this has permitted relatively low rates of ethephon use. However, when temperatures are high, this high breakdown rate may be a disadvantage and sometimes, when field conditions are adverse, better inductions can be obtained with a solution pH of only 7 (Sinclair, 1991). Application between dusk and dawn, when temperatures are cooler and stomata are open, increases the effectiveness of ethephon, presumably because ethyl-

ene released by ethephon decomposition outside the plant is absorbed through the stomata. Two applications spaced 4–8 days apart may be required to force a high percentage of plants.

Prevention of natural flowering

When sensitivity to natural induction is high in subtropical regions, inhibiting natural induction can be a greater concern than is forced flowering. As the pineapple fresh-fruit industry has expanded, it has become common to force pineapple crops in all months of the year. As a result, natural induction before the scheduled forcing date has become a significant problem. In some areas, particularly subtropical regions, and in some years, precocious flowering may cause serious yield losses because it results in fruit that are too small or too few in number to be worth harvesting. Natural induction is less likely to be a problem in warm, humid, tropical environments. As noted previously, some intervarietal hybrids are more susceptible than 'Smooth Cayenne' to natural induction. As hybrids replace 'Smooth Cayenne' in fresh-fruit production, natural induction is likely to become more, rather than less, important.

Cultural controls

During the time of year when natural induction normally occurs, cultural practices provide some degree of control over this process. These controls consist of ensuring that only relatively small, rapidly growing plants are in the field when natural induction is most likely to occur. Plants that are to be forced into flowering a few months after natural induction normally occurs should be grown with optimum levels of nutrients and water to minimize stresses and promote rapid vegetative growth.

Plant-growth regulators

Synthetic auxins, such as NAA, force flower induction of pineapple at low concentrations while higher concentrations of these auxins delay it (Collins, 1960; Gowing and Leeper, 1960). Recent research with 2-(3-cholorophenoxy)-propionic acid (3-CPA) (Scott, 1993; Rebolledo-Martinez *et al.*, 1997; Rabie *et al.*, 2000; Rebolledo *et al.*, 2000) and certain triazole growth inhibitors (Min and Bartholomew, 1996; G. Taniguchi, 1998, personal communication) shows that there is some potential for inhibiting natural flowering with plant growth regulators, but inhibition is not complete and plant injury can sometimes occur. At present, no plant-growth regulator has been found that is completely effective in inhibiting natural flowering and no chemical is known to be registered for this process.

Genetic engineering

Genetic engineering of a clone with reduced production of ethylene may also provide a method for controlling natural flowering (see Smith *et al.*, Chapter 4, this volume). If antisense or trans-switch technology could be used to turn off the gene that codes for the ACC synthase associated with natural flower induction, then transformed plants would presumably not produce sufficient ethylene to initiate flowering. The key to this approach is to target the specific gene associated with natural flower initiation without affecting other ethylene-related processes in the plant.

Inflorescence and Fruit Development and Yield

Introduction

The critical factors that determine fruit yield include the plants per unit area, the number of fruits harvested from those plants and the average fruit weight. At a given plant population density, the potential number of fruits available for harvest is determined by the number of plants that produce an inflorescence, the number of those fruits that mature and the number of fruit actually harvested. The cost of harvesting often dictates the percentage of fruit actually harvested, and losses commonly average 13%, with a range

of 5–30% (Wassman, 1982). Even when harvesting fruits from fields of a few hectares, it can be uneconomic to have a harvesting crew visit the field with sufficient frequency to harvest every fruit that matures. The lowest losses are associated with fields with the least spread in maturity and requiring only one picking, while the greatest losses are associated with fields where up to ten picks are required. Ethephon can be used to hasten 'ripening' of the fruit (see below), which may sharpen the harvest peak and increase recovery of fruit from the field, but it can also reduce average fruit quality and increase the variation in maturity and quality at the time of harvest.

Within a given environment, fruit weight at harvest is determined in large part by plant weight at forcing (Py and Lossois, 1962; Gaillard, 1969; Tan and Wee, 1973; Malézieux, 1988; Malézieux and Sébillotte, 1990a). However, other critical factors that affect average fruit weight per plant include the success of inflorescence induction, the quality of this physiological process in terms of the number of fruitlets initiated per unit of plant weight and the fruit-filling process(es). At maturity, average fruit weight is determined by the number of fruitlets formed during inflorescence induction and the average fruitlet weight.

Most of the factors associated with yield can be managed to some degree. The discussion below covers, to the extent that information is known and available, those factors that influence the quality of forcing and the physiology of fruit development and how factors such as plant weight at forcing and plant population density determine yield.

Resource allocation

Few studies of carbohydrate allocation or reallocation in pineapple during reproductive development were found. During vegetative growth, the dominant carbohydrate sinks are the young leaves and the roots, and there is an allometry between the leaves and the stem (Malézieux, 1988). There is little increase in stem length or diameter once flowering has been initiated, but experiments conducted in Côte d'Ivoire and Hawaii show that stem growth rate, on a dry-weight basis, and starch accumulation increase rapidly after flower initiation (see Fig. 5.11; H.Y. Young, 1965, personal communication; Malézieux, 1993; E. Malézieux, 1993, unpublished results). In Hawaii, starch in the stem, on a dry-weight basis, increased from about 15% 9 months after planting to over 60% midway through the fruit development period some 10 months later. Leaf starch on the same basis increased from less than 2.0% to about 8.0% during this same time period. While the change in starch concentration in leaves is relatively small, when multiplied by the large amount of leaf weight present, it represents a large storage reserve.

A surplus of starch in the plant during early reproductive development probably results from a lack of new sinks during this phase, as no new leaves are initiated and the fruit does not yet represent a significant sink for carbon. About 100 days after forcing in Hawaii and sooner in Côte d'Ivoire, where temperatures are warmer and fruit growth is more rapid, there is a decrease in stem dry matter (see Fig. 5.11) and probably in stem starch, or both, indicating mobilization of starch from the stem to help meet fruit carbon demand. In Hawaii, leaf starch is apparently also mobilized to meet the increasing demand from the rapidly developing fruit. The intensity and importance of reallocation of assimilates from the stem and leaves to the fruit may depend on climate (irradiance, drought) during fruit filling and on carbon balance between source (assimilates produced) and sinks. Reallocation was greater for large than for small plants in Côte d'Ivoire (Malézieux, 1993), presumably because, with a higher dry-matter content and possibly higher starch, there was more substrate to reallocate.

Data from Australia, Côte d'Ivoire and Hawaii clearly show that the developing fruit is a stronger sink than are the suckers. When flower induction occurs, apical dominance over axillary buds is broken and destructive sampling soon after induction shows a few to several axillary buds beginning to grow. However, in the warmer tropics, sucker development is typically delayed,

i.e. no visible suckers form, until after the fruit has matured. In all regions where pineapple is grown, sucker development may also be delayed where plants are small and in fields with high plant population densities. In subtropical areas, such as Australia and Hawaii, the situation is more complicated. In these cooler climates, the date of forcing typically determines the size of the fruit. Forced induction in the winter months – November until at least January in Hawaii and June to August in Australia – tends to produce smaller fruit on a plant of a given size than does forcing during warm summer months, when irradiance is high. These somewhat smaller fruit develop and mature during the warm spring and summer months when temperatures are warm and irradiance is high. Because photosynthetic leaf area is large relative to the size of the developing fruit, we speculate that photosynthetic capacity exceeds carbohydrate demand by the developing fruit, so there is surplus carbohydrate available for sucker growth. Thus, suckers initiated at forcing develop along with the fruit. In southern Queensland, Australia, suckers on plants from which fruit is harvested in summer can become large enough to shade the fruit. The converse of this situation occurs when forcing occurs in January–February in Australia and in the midsummer months in Hawaii. Fruits initiated during this time are large relative to plant size, presumably because high rates of photosynthesis provide the energy required to initiate large numbers of fruitlets. These relatively large fruit mature and ripen during cool weather, when irradiance is near a minimum. Sucker development on such plants is delayed, presumably because the leaves do not have sufficient photosynthetic capacity to support both the developing fruit and sucker growth. In Australia, the time after initiation at which suckers between 5 and 40 g weight were first seen in a time-of-planting trial depended on the month in which forcing occurred. Forcing in January resulted in the longest interval before suckers appeared (295 days), while plants forced in September and October produced suckers in the shortest time, about 100 days (Sinclair, 1992a).

Defoliation experiments clearly show the importance of leaf area and weight to the developing fruit, slips and suckers. A. Hepton (personal communication) showed that the weight of fruit, slips and suckers all increased linearly the closer to harvest plants were defoliated (Fig. 8.5). It is clear that anything that decreases carbon assimilation by leaves, such as reduced irradiance or decreased effective leaf area, will reduce yield and the size and number of shoots available for propagation.

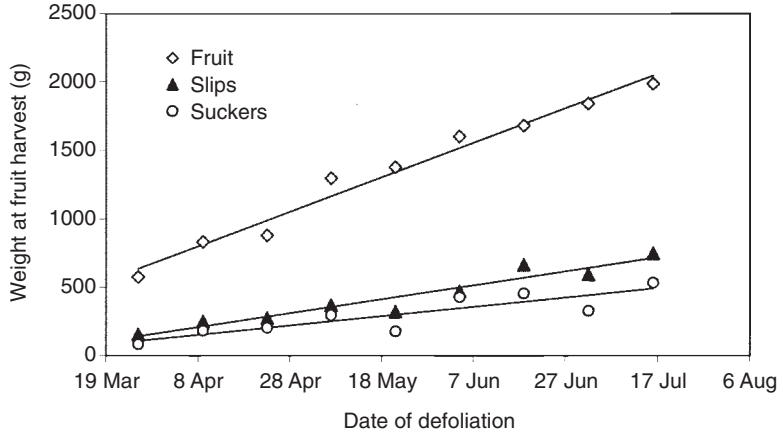

Fig. 8.5. Effect of date of leaf defoliation on mean fruit, slip and sucker mass at the date of fruit harvest. For fruit, $y = 636.4 + 12.57x$, $R^2 = 0.98$; for slips, $y = 141.2 + 5.11x$, $R^2 = 0.92$; for suckers, $y = 106.5 + 3.42x$, $R^2 = 0.76$; $n = 9$ for all. (Data from A. Hepton, personal communication.)

Temperature

The rate of fruit growth over time and the duration of the development phases described previously are mainly determined by temperature. Development from the time of induction to the stage 1.3 cm (½ in.) open heart is well correlated with cumulative thermal time based on daily maximum (T_{max}) and minimum (T_{min}) air temperature (Fleisch and Bartholomew, 1987) by the equation:

$$\text{Cumulative thermal time} = \Sigma\ (T_{max} - T_{min}) \quad (1)$$

Once the inflorescence emerges in the centre of the plant, development is less well correlated with thermal time based on air temperature and is better related to fruit thermal time (Malézieux *et al*., 1994), which is at least partially dependent on irradiance. Exposure to direct sunlight elevates fruit temperatures, and such temperatures in the exposed section of the fruit can exceed 50°C at ambient air temperatures of 30°C or less (Nightingale, 1942; Van Lelyveld, 1957; Soler, 1992). The difference in surface temperature between the sunny and shaded faces of the fruit can reach 13°C (Teisson, 1973). These high temperatures and temperature gradients can hasten the rate of fruit development (Zhang, 1992), though, in hot environments, very high fruit temperatures may retard fruit development. A simulation model, based on daily maximum and minimum temperature and heat-unit accumulation, which takes into account fruit temperature and above-optimum temperatures, was developed that could predict harvest dates with reasonable accuracy in Queesland, Australia, Côte d'Ivoire, Hawaii and Thailand (Malézieux *et al*., 1994).

A developmental disorder referred to as 'prickly eye' is apparently related to cool temperature or to reduced irradiance, or both. Fruitlets of fruits that begin development during the colder months in Australia, and sometimes in Hawaii, do not fill out normally and the fruitlets are conical in shape at maturity (Swete Kelly and Bartholomew, 1993). Because such fruit mature during the spring and early summer, they are of excellent quality, but, because they do not fill out properly, average fruit weight and yields are reduced significantly (Swete Kelly and Bartholomew, 1993).

As was noted earlier, variations in temperature associated with latitude (Glennie, 1981), altitude (Aubert *et al*., 1973; Table 5.1, Chapter 5, this volume) and season (Wassman, 1986) can induce great differences in the length of the crop cycle. In humid tropical climates, such as Côte d'Ivoire (Malézieux and Lacoeuilhe, 1991) and Cameroon (Gaillard, 1970), variations in the interval from forcing to harvest may range from a minimum of 140 days for plants forced in February to a maximum of 160 days for plants forced in June, with an average of only 10 days between the maximum and minimum interval. In the somewhat cooler climate of Madagascar, the interval from forcing to harvest ranges from 144 days during summer to 221 days during winter (Moreau and Moreuil, 1976). In Hawaii, the interval from forcing to harvest for 'Smooth Cayenne' ranges from about 180–220 days near sea level and from 220 to at least 270 days at 800 m, resulting in seasonal variation ranges of about 40 days (180–220) near sea level to about 50 days (220–270) at 800 m. Most of this variation is accounted for by differences in mean temperature during the period of fruit development, which are predictable (Zhang *et al*., 1997). Over the region where pineapple is grown, days from forcing to maturity range from 140 to 150 (minimum value) in Côte d'Ivoire (Malézieux and Lacoeuilhe, 1991) and Cameroon to 280–300 days in Queensland (Wassman, 1986; Sinclair, 1992a) and South Africa (Smith, 1977).

In subtropical regions, the fruit development period is more variable. In several time-of-planting studies where fruiting was forced, the interval from forcing to harvest was somewhat to much longer during seasons with cool temperatures (Dalldorf *et al*., 1975; Moreau and Moreuil, 1976; Smith, 1977; Wassman, 1990). In southern Queensland (27°30'S–26°S), the days from forcing to harvest can range from about 180 (September induction/April harvest) to 280 (April induction/January harvest) (Wassman, 1990; Sinclair, 1992a) and similar

data were developed up to 23°S latitude (Wassman, 1974).

In addition to delaying development, high and low temperatures can directly injure fruits, causing significant losses. Frost injury can occur in cool subtropical climates and the extent of injury determines whether or not a fruit can be processed. Frost-injured fruit are unmarketable as fresh fruit (Swete Kelly and Bartholomew, 1993).

Fruit sunburn occurs during periods of high irradiance and can result in significant losses of fruit. Sunburn occurs when a localized area of the fruit is directly irradiated by the sun at a sharp angle of incidence, resulting in elevation of flesh temperatures above the thermal death point. Sunburn injury occurs most often when fruit lodge and the large, dark-coloured surface is exposed to direct irradiation from the sun, but can occur any time when temperatures are hot and irradiance is high. Sunburn injury can merely discolour the shell or cause such severe injury that the fruit is unusable (Py *et al.*, 1987). Sunburn during inflorescence development can produce fruit that are severely misshapen, and this type of injury is reported to be much more prevalent on calm days (Swete Kelly and Bartholomew, 1993). When mature fruit are severely sunburned, the injured area becomes translucent and may become desiccated. Ratoon fruit are more likely to be affected than are plant-crop fruit because they are more prone to lodging (Py *et al.*, 1987; Swete Kelly and Bartholomew, 1993). A more general 'cooking' of the fruit is associated with very high air temperatures, usually about 40°C. This latter type of injury has apparently only been observed in Queensland, Australia. Fruit cooking results in fruit that are pale white or translucent around the core, in the same pattern as is seen in postharvest chilling injury, and the fruit are generally very spongy. Both sunburned and cooked fruit are rejected for processing in Australia.

Irradiance, slope and aspect

Though few controlled studies were found, the available data indicate that fruit weight is positively correlated with increasing solar irradiance (Bartholomew and Malézieux, 1994). Artificial shade delayed fruit development in Hawaii (Sideris *et al.*, 1936), but it seems likely that shading reduced fruit temperature, thus slowing the rate of development. Covering both the fruit and crown reduced starch accumulation in the stem of the crown relative to stems of uncovered crowns (Sideris, 1933). The data allow the conclusion that crowns become autotrophic and sunlight exposure is required for starch accumulation in the crown stem. Starch reserves in planting material are considered to be an important factor in establishment (see Hepton, Chapter 6, this volume). Shading due to interplant competition reduces the weight of fruit from the centre row of three-row plantings below that of adjacent rows, and removal of plants at the time of forcing, when vegetative weight is fixed, increases the fruit weight (Bartholomew and Malézieux, 1994). In a plant-removal experiment in Côte d'Ivoire, planting densities of 50,000 and 100,000 plants ha^{-1} were established (Malézieux and Sébillotte, 1990c). At the time of forcing, every other plant was removed in half of the plots. Plant removal significantly increased fruit weight by 50 and 14% in the high- and low-density treatments, respectively. Similar results were obtained in Hawaii (W.G. Sanford, 1966, personal communication). Since plant weight in all plots was equal at the time of forcing, the improved exposure of plants in plots where plants were removed at the time of induction resulted in increased fruit weight. Increased fruit weight resulted from an increase in fruitlet weight in Côte d'Ivoire, while in the Hawaii study, increased fruit weight resulted from a significant increase in fruitlet number (Sanford, 1962). The differences between the two studies may be explained by the cooler temperatures prevailing in Hawaii, which would prolong the period of fruitlet initiation and thus allow enhanced rates of photosynthesis to be reflected in the number of fruitlets initiated.

In Côte d'Ivoire, where temperature is relatively stable and irradiance fluctuates significantly with seasonal changes in cloud

cover and rainfall, potential plant weight at forcing and fruit weight at harvest were correlated with irradiance intercepted during the vegetative growth period and for the entire cycle (Fig. 8.6; Malézieux, 1988). In these unirrigated conditions, yield was depressed when drought was prolonged. Seasonal changes in irradiance increase with distance north and south of the equator and the effect of such changes on pineapple growth and yield are probably confounded with simultaneous changes in temperature. Southern Queensland, Australia and South Africa are further from the equator than most pineapple-growing regions and large seasonal effects on crop and fruit characteristics are observed in both regions. In southern Queensland (D. Christensen, 1999, personal communication), there is an approximately 2-month difference in time from flowering to fruit maturity between fruit induced in April and maturing over winter (9 months) and fruit induced in October and maturing over summer (7 months). In winter when the sun angle and total irradiance are low, plant layout in the field can affect fruit maturity. D. Christensen (1999, personal communication) observed that, where two-row beds were planted in an east–west orientation, plants in the north-facing row made greater growth than shaded plants in the south-facing row of two-row beds. Differences in the rate of fruit development in fields forced on the same day that have both north- and south-facing slopes help growers to manage peak harvests because areas with north-facing slopes mature about 2 weeks earlier than those with south-facing slopes (D. Christensen, 1999, personal communication). While there is only limited direct evidence of an effect of irradiance on yield, a wide range of experience indicates that growth, yield and fruit quality are all poorer when irradiance is limiting.

Drought and water excess

Few quantitative studies of the effects of drought on fruit development were found. E. Malézieux (1992, unpublished results) found that the expected fruitlet number was reduced by drought, and Chapman *et al.* (1983) reported that prolonged drought of pineapple grown in pots reduced fruit weight to the extent that it was commercially unacceptable. If stress occurs during fruit development, the peduncle can become shrivelled and the fruit may lodge or break off (Swete Kelly and Bartholomew, 1993).

In Côte d'Ivoire, the fruit weight of plants grown in the field was related to the percent-

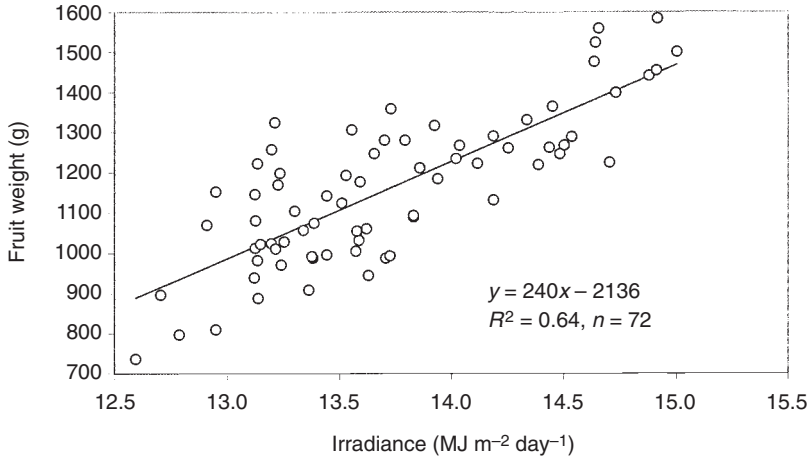

Fig. 8.6. Effect of mean irradiance from planting to harvest on average fruit weight of 'Smooth Cayenne' pineapple. Data are means of 60 fruits harvested from 72 monthly plantings in Côte d'Ivoire during a 6-year period. All plants were forced 8 months after planting. (Redrawn from Bartholomew and Malézieux, 1994.)

age of water requirement provided by irrigation between flowering and harvest (Combres, 1980). A 17% decrease in fruit weight occurred when only 20% of the plant water requirement was provided during this period. In Côte d'Ivoire, a dry period that occurs during the month after forcing can reduce the number of fruitlets and a drought that occurs at the end of fruit development reduces fruitlet weight (E. Malézieux, 1992, unpublished results). Average fruit-weight differences at harvest between irrigated and unirrigated plots can reach 750 g when the dry season is severe (Combres, 1983). Yield increases of 30% due to biweekly irrigation during fruit development were obtained in Taiwan (Huang and Lee, 1969). In Côte d'Ivoire, yields were 12–15 Mt ha^{-1} greater with irrigation in a normal year (Combres, 1979; Malézieux and Sébillotte, 1990b) and 25–30 Mt ha^{-1} greater when drought was severe (Combres, 1979). While Huang and Lee (1969) reported that irrigation had no effect on fruit quality, Linford and Magistad (1933) found translucence was greater and acidity was decreased in fruit from irrigated plots. Beyond the effects on vegetative growth and fruit development, drought can also reduce sucker production (Medcalf, 1950), and reductions of up to 50% were observed at the end of the dry season (Combres, 1979).

While few quantitative data on the effects of water excess on growth under field conditions were found, yields were reduced by 15% (about 10 Mt of exportable fruits) in Côte d'Ivoire when plants were irrigated at 140% of the water requirement for the period between flowering and harvest (Combres, 1983). Until recently, when good fungicides became available to control *Phytophthora* spp., loss of plants to root and plant rots was a greater concern than reduced growth due to waterlogging (Rohrbach and Apt, 1986; Rohrbach and Johnson, Chapter 9, this volume).

Wind

No papers were found that reported on the detrimental or beneficial effects of wind on pineapple. In Hawaii, where strong northeasterly trade winds can exceed velocities of 15 m s^{-1} (about 56 km h^{-1}), wind damage of plants is negligible and no fruit damage has been reported. Wind can remove large amounts of heat and may reduce the incidence of malformed or multiple crowns. Wind can also transport large amounts of heat away from large fruit, which would help to reduce their internal temperature and may be very important in reducing the incidence of sunburn during hot periods of the year.

Plant population density and plant size

Effect of plant population density on average fruit size and yield

The effects of planting density, and thus of competition for light, on average fruit weight and yield have been demonstrated many times (Bartholomew and Paull, 1986; Py *et al.*, 1987) and have been reconfirmed by recent studies (E. Malézieux, 1992, unpublished results; Scott, 1992; Zhang, 1992; Christensen, 1994). Virtually all studies show that average fruit weight decreases approximately linearly with increasing planting density (Bartholomew and Paull, 1986; see Fig. 6.10), while yield increased linearly or in a curvilinear manner if densities were high enough (see Fig. 6.11). Fruit diameter (Treto *et al.*, 1974; Zhang, 1992) and fruit length (Norman, 1978) decreased as the planting density increased. Although yield components were not reported in most studies, over a moderate range of densities the decrease in fruit weight seems to be due mainly to a decrease in average fruitlet weight rather than in fruitlet number (Sanford, 1962; Pinon, 1981; E. Malézieux, 1992, unpublished results). However, at very high densities, fruit are so small that it is likely that both fruitlet number and weight decrease. In recent studies (Scott, 1992; Zhang, 1992; Christensen, 1994), total yield increased with planting density to populations as high as 128,000 plants ha^{-1}, but the numbers of smaller fruit, which have a lower commercial value, increased at the highest densities. All varieties of pineapple examined respond similarly to increasing plant population density, although the slopes

of the lines fitted to the data were different for 'Queen', 'Spanish' and 'Smooth Cayenne' (see Fig. 6.10). The differences in slope are probably due in part to differences in the efficiency of plants in producing a fruit, but differences such as those for 'Smooth Cayenne' grown at different locations are probably due largely to differences in environment or cultural practices.

Effect of plant population density on crop duration and spread in maturity

The period from forcing to harvest is prolonged as planting density increases (Py *et al*., 1987; Scott, 1992; Zhang, 1992; D. Christensen, 1994, personal communication). In Hawaii (Zhang, 1992), when plants were forced in September, no delay in maturity was found at plant population densities below 75,000 plant ha^{-1}. In southern Queensland, days from induction in January, 1990 to peak harvest increased from 253 at a density of 46,100 plants ha^{-1} to 265 at a density of 80,700 plants ha^{-1}. A second study in 1994 had similar results, with days from induction to harvest increasing from 256 at 62,500 plants ha^{-1} to 272 at a density of 85,200 plants ha^{-1}. Christensen (1995) found that there was about a 1-day delay in maturity for every 1000 plant ha^{-1} increase in density, though presumably there is a lower threshold where this effect is not observed.

Christensen (1995) reported that peak harvest was not determined at a density of 93,700 plant ha^{-1} because plants segregated into two populations, one of large, unshaded fruit that matured early and one of small, shaded fruit that matured much later. This segregation was probably due to the increased plant-to-plant variability that occurs at high plant population densities. Small variations in plant weight at planting become magnified as density increases because large plants overtop smaller ones. Development of small fruit buried in the canopy are delayed because such fruits have less sun exposure than do large fruit borne on large plants. Shading could retard development by lowering the average fruit temperature (Malézieux *et al*., 1994) or by reducing the supply of assimilates allocated to the developing fruit. It is clear that fruit development is delayed, particularly where higher plant populations densities are used.

Plant-weight–fruit-weight relationships

Plant or leaf weight at the time of forcing and fruit weight at harvest are generally highly correlated for a given variety of pineapple within a given environment (Bartholomew and Paull, 1986; Py *et al*., 1987; Malézieux, 1988, 1993; Zhang and Bartholomew, 1997). However, the relationship between plant weight at induction and fruit weight at harvest is complex and not always predictable. The strength of the relationship between plant or 'D'-leaf weight and fruit weight depends on the growing conditions, including climatic conditions, prevailing during a specific crop and hence it is not extrapolatable. Linford (1933) reported that the number of floret buds on plants from two fields was well correlated with stem and peduncle diameter, but less well correlated with stem weight and not significantly correlated with stem length. Further, the number of florets was greater for each stem-diameter class for plants from one field than from the other. Stem weight per floret was 1.65 g for plants from one field and 10.45 g from the second field, causing Linford (1933) to suggest that the factors that determine floret numbers may not be proportional to the plant's ability to carry its fruitlets to maturity.

In regions near the equator, where the environment is relatively uniform throughout the year, the correlation between plant or 'D'-leaf weight at forcing and fruit weight at harvest might be expected to be high during most months of the year. However, in Côte d'Ivoire, within a particular field variability in fruit weight might or might not be well correlated with plant weight at forcing (Malézieux, 1988). In these equatorial regions, it seems likely that the primary effect of plant weight is to determine fruitlet number rather than fruitlet weight at harvest (Malézieux, 1988). In an experiment where plants of different ages, and consequently plant weights, were forced at the same date (Malézieux and Sébillotte, 1990a), the

increase in plant weight at forcing was associated with an increase in fruitlets per fruit (Fig. 8.7). The leaf-area index (LAI) in this experiment ranged from 2.0 to 10. The number of fruitlets in this experiment was linearly correlated with plant growth during the month following forcing (Fig. 8.8).

A positive and significant relationship between plant weight and fruitlet number was also shown in an experiment in Côte d'Ivoire, where plots planted monthly where forced systematically at 8 months (Malézieux and Sébillotte, 1990b). Part of the residual variation might be related to climatic conditions in the month following forcing, because drought and low radiation reduced the expected number of fruitlets (Fig. 8.9). The fact that there was no direct relationship between plant weight at forcing and fruitlet weight at harvest in these experiments might be related to the fact that fruitlet filling is the result of the balance between the source (whole-plant capacity to provide assimilates for the fruit) and the sink (number for fruitlets to be filled).

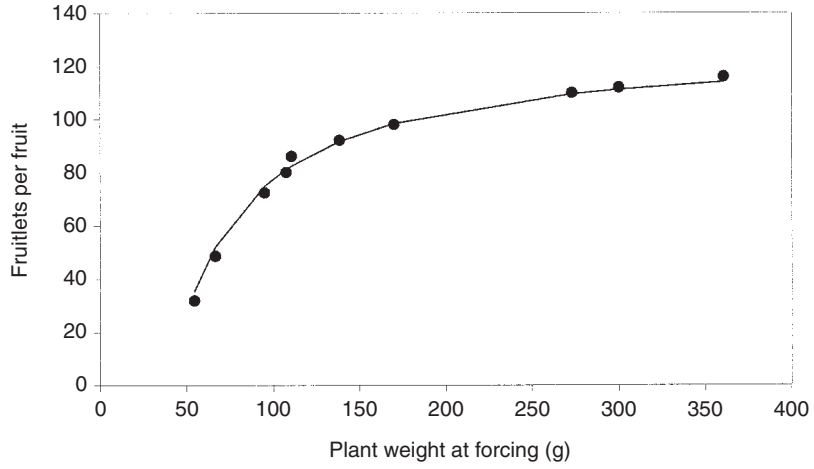

Fig. 8.7. Effect of plant weight at forcing, dry-mass basis, on fruitlets per 'Smooth Cayenne' fruit grown in Côte d'Ivoire (from Malézieux and Sébillotte, 1990a).

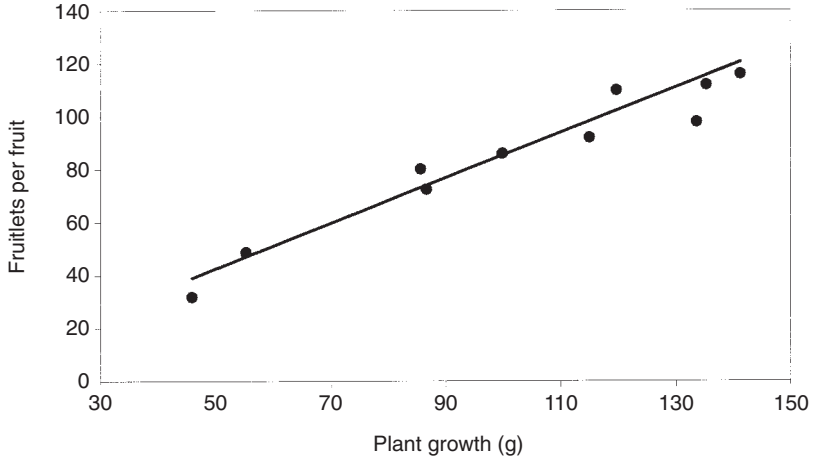

Fig. 8.8. Relationship between plant growth in the month following forcing and fruitlets initiated per fruit in Côte d'Ivoire (from Malézieux and Sébillotte, 1990a).

Statistical relationships between plant weight at forcing and fruit weight at harvest may also be established. In Côte d'Ivoire, a linear relationship was found for the data obtained from the monthly-planting trial previously referred to (Malézieux, 1993; Fig. 8.10). Part of the residual variation may be explained by climatic conditions after forcing, which influence fruitlet number and fruitlet filling. Data points that fall below the regression line are due to inadequate fruit filling for plantings made in May, June and July, because of drought and low irradiance during fruit development, while data points located above the line are due to good growing conditions during fruit development for plantings made in January and February. This relationship is not universal, but depends on a variety of factors including the climatic conditions prevailing after forcing,

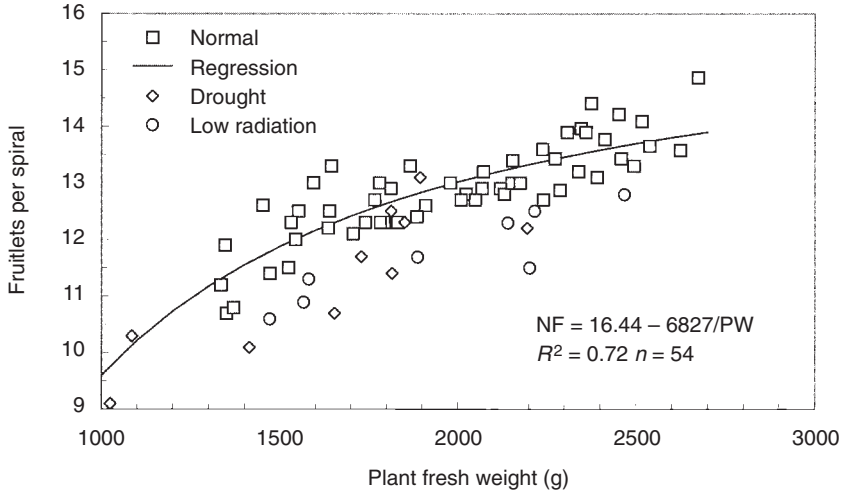

Fig. 8.9. Relationship between plant fresh weight (PW) and fruitlets per long spiral (NF) for 'Smooth Cayenne' pineapple grown in Côte d'Ivoire (from Malézieux and Sébillotte,1990b).

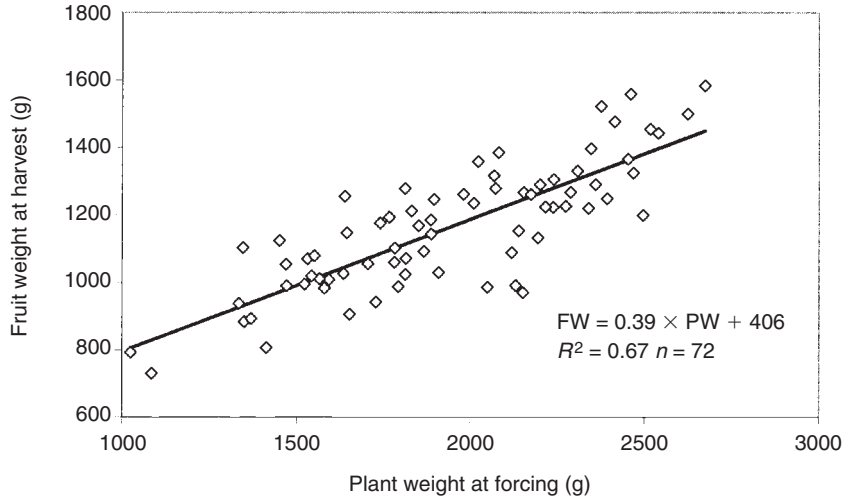

Fig. 8.10. Relationship between plant fresh weight at forcing (PW) and fruit weight at harvest (FW) for 'Smooth Cayenne' pineapple in Côte d'Ivoire (from Malézieux, 1993).

the mineral status of the plant and the quality of pest and disease control.

In a time-of-planting trial conducted in Queensland, Australia (Sinclair, 1992b), which included multiple dates of forcing, the relationship between plant weight at forcing and fruit weight at harvest was not significant if no account was taken of season of induction. Seasonal influence was a major determinant of fruit weight in this experiment. Fruit weight was mainly determined by climatic factors – primarily temperature – that occurred during flower induction and fruit development rather than plant weight at forcing (Sinclair, 1992b). In this trial, plants weighing 3.0 to almost 4.5 kg that were forced in autumn had low (1.0 kg) fruit weight at harvest because fruit development occurred during the winter. Plants weighing only about 2.5 kg that were forced in spring produced fruit that had a fresh weight of about 2.0 kg at harvest.

Genetic effects

Some genetic variation in the length of the fruit development period exists within hybrids (Chan and Lee, 2000), though it was apparently not great enough to significantly shorten time from forcing to fruit maturity. Variation in length of the fruit development period has also been found in 'Smooth Cayenne'. In Queensland, a comparison of four clones indicated that 'Smooth Cayenne' clone 'C10' matured approximately 7 days earlier than the 'Smooth Cayenne' clone 'F180'. The Pineapple Research Institute of Hawaii hybrid 53–116 matured approximately 14 days later than 'C10' (G.M. Sanewski, 1996, unpublished results). In the same environment, cultivars of 'Queen' typically mature 4–6 weeks earlier than 'Smooth Cayenne'.

Crown Development

Crown size

Little work has been done on the growth of the crown and the factors that influence it, especially where fruit development has been induced throughout the year. Near the time of fruit harvest, crown length, weight and leaf number reach a maximum, and the crown is said to enter a state of dormancy (Py *et al.*, 1987). This dormant state probably lasts only as long as the crown remains attached to the fruit, because stem etiolation has been observed in crowns stored for prolonged periods of time and new roots are initiated rapidly when fresh crowns are planted in a favourable environment.

Crown weight tends to be small on fruit that develop in the tropics (Py *et al.*, 1987), and this effect was attributed to the relatively short interval between induction and fruit harvest. Crown weight varies considerably throughout the year in Hawaii. Fruit initiated in winter tend to be small relative to plant weight. These relatively smaller fruit mature in summer, when irradiance and temperature are high, and tend to have large crowns. Plants that bear a small fruit during summer would probably produce a surplus of carbohydrate in the warm temperatures that could be allocated to the developing crown before it becomes autotrophic. Surplus carbohydrate, warm temperatures and high irradiance would speed crown growth and presumably result in a larger and heavier crown at harvest. Fruit initiated in Hawaii in summer, when temperatures are warm and irradiance is high, tend to be heavier relative to plant weight than those initiated during the winter. These fruit develop and mature in winter, when temperatures are cool and irradiance is low. Such fruit generally have small crowns, presumably because plants bearing relatively large fruit during winter would have a more limited supply of photosynthate to allocate to the strongest sink. There would probably be little surplus carbohydrate available to the developing crown, so crown development would be delayed by lack of substrate and by low temperature and irradiance.

Multiple crowns

Multiple crowns are a common disorder that can be of genetic or environmental origin. Multiple crowns increase the size of the fruit

core and result in flattening of the upper portion of the fruit, which reduces the value of the fruit for the fresh market and for canning. Collins (1960) states that fasciation – an abnormal growth resulting in two to numerous crowns – is relatively uncommon in 'Smooth Cayenne' and 'Queen,' but common in 'Singapore Spanish' and 'Pernambuco'. Collins (1960) also reported the existence of mutant clones of 'Smooth Cayenne' that produced 50% or more fruit with multiple crowns.

Environmental conditions that promote the multiple-crown disorder are high fertility and rapid growth following a period of prolonged drought, if such conditions occur about the time of inflorescence initiation (Collins, 1960; Py *et al*., 1987). An increased incidence of multiple crowns is correlated with periods of high irradiance and high temperature that occur during early inflorescence development, although the disorder is generally thought to be due to high temperature injury. Increased planting density reduced the incidence of multiple crowns (Linford and Mehrlich, 1934; Norman, 1977; Scott, 1992), presumably because mutual shading in the more dense plantings reduced the temperature of the reproductive apex. The significance of this shading effect is confirmed by the observation that there was a higher incidence of deformed crowns on outside rows than in the interior of a field. Irrigation during inflorescence development reduced the incidence of multiple crowns (Py *et al*., 1987).

Fruit Enlargement

Synthetic auxins such as NAA, β-naphthoxyacetic acid and 3-CPA applied after inflorescence emergence, and most often after flowering, increase fruit weight at harvest (Bartholomew and Criley, 1983), and fruit yields can be increased by up to 40% (Williams, 1987). The available literature indicates that only 3-CPA was used on a commercial scale. A possible added advantage of 3-CPA is that it reduces crown size, which is a particular benefit for fresh-fruit production. The hazards of growth-regulator-induced fruit enlargement include delayed harvest, decreased shelf-life, crown damage, decreased total soluble solids (TSS), pale flesh colour, increased incidence of disease and increased numbers of green-shell ripe fruit (Bartholomew and Criley, 1983; Williams, 1987). The risks associated with the use of 3-CPA appear to outweigh its benefits and, as a consequence, it is not registered for use in Hawaii and has been banned from use by growers providing fruit for the cannery in Queensland. However, it is still used to enlarge fruit of 'Queen' pineapple in Malaysia.

Predicting Fruit Development and Yield

It is possible to predict the rate of plant growth, fruit development and yield in relation to environmental factors and cultural practices by simulating plant development (leaf appearance and fruit phenology), carbon assimilation and allocation to various plant parts using integrated modelling techniques. ALOHA-Pineapple (Zhang and Bartholomew, 1993; Zhang *et al*., 1997) is a pineapple crop model that simulates pineapple growth, development and yield on a daily time-step basis in different environments. A flow chart of the major factors incorporated into the model that affect pineapple growth, development and yield are summarized in Fig. 5.17. The model was calibrated and validated using data from Australia, Côte d'Ivoire and Hawaii and takes into account temperature, irradiance and plant–soil water relations. Nutrition effects, such as nitrogen, remain to be introduced into the model. The model was developed using the structure and format of the CERES-maize model (Jones and Kiniry, 1986) and works under the IBSNAT-DSSAT shell (Anon., 1994).

Fruit growth of 'Smooth Cayenne' has been studied fairly intensively and it is a highly predictable process up to the time the developing fruit becomes visible. Development progresses with increasing thermal time from forcing until about the time the 1 cm open-heart stage is reached (Fleisch and Bartholomew, 1987; Malézieux *et al*., 1994;

Zhang *et al.*, 1997). Thermal time is calculated as the sum of daily mean air temperature minus a basal temperature below which it is assumed that no development occurs. For modelling purposes, the basal temperature was set at 10°C (Malézieux *et al.*, 1994). After the inflorescence emerges, and especially after anthesis begins, fruit development is more difficult to predict. It is assumed that this is due to the absorption of solar radiation during the day, which can significantly elevate fruit temperature above air temperature (Bartholomew and Malézieux, 1994). For the period from flowering to fruit maturation, fruit growth and maturation were best predicted by fruit thermal time calculated from estimates of fruit rather than air temperature (Malézieux *et al.*, 1994). Direct absorption of solar radiation raises fruit temperature well above air temperature (Bartholomew and Malézieux, 1994) and apparently hastens the development rate up to some optimum temperature. Above that optimum, fruit development can be delayed (Malézieux *et al.*, 1994). While it is clear that solar irradiance elevates fruit temperature, the relationship between irradiance and fruit temperature, and especially average fruit temperature, has not been adequately characterized. It also seems likely that fruit temperature declines somewhat with increasing wind speed, but no data were found on the subject.

Detailed data on the effects of nutrition on rate of development were not found, but Py (1955) reported that fruit development took longer where N was high without K than was the case for a balanced fertilizer.

Ratooning

Ratooning is the production of one or more crops on the same plant without replanting. Ratoon-crop production eliminates several steps in the production process, including land preparation, preplanting fertilization, pest control practices and planting. Cost savings can be considerable and the ratoon crop, if well grown, may be the primary source of profit for a large plantation. It is an axiom that the quality of the ratoon crop is determined by the quality of the mother-plant root system at the time of harvest. Failure to maintain a vigorous, healthy root system for the ratoon is almost certain to result in failure of the ratoon crop. Regardless of the quality of plants entering the ratoon-crop cycle, ratoon yields are usually less, more variable and have a smaller average fruit size than does the mother-plant crop. It may be possible to produce two or more ratoon crops, but good pest- and disease-control practices and adequate nutrition are essential to ensure the success of the ratoon crop (Py *et al.*, 1987).

The source of the ratoon is one or more vegetative shoots, which begin to develop on the mother-plant shoot before, in the case of 'Queen Victoria', or after, in the case of 'Smooth Cayenne', natural induction or forcing (Maerere, 1997). Maerere (1997) concluded that apical dominance of 'Queen Victoria' was weak, while that of 'Smooth Cayenne' was strong. No studies of the effects of plant population density or environment on sucker development of 'Queen Victoria' were found, whereas a relatively large number of such studies exist for 'Smooth Cayenne'. However, the tropic-wide implications of these studies have not been evaluated. The extent to which 'Smooth Cayenne' suckers develop with the fruit is an issue of carbohydrate allocation. While sink strength in pineapple has not been examined directly, circumstantial evidence leaves little doubt that the fruit is a stronger sink for carbohydrates than are the suckers. Thus, any cultural or environmental factor that results in an insufficiency of carbohydrate for fruit development will delay sucker development. It has been known for many years that 'Smooth Cayenne' pineapple stems contain significant starch reserves (Sideris and Krauss, 1936; see Malézieux *et al.*, Chapter 5, this volume), but their significance has not been well studied. Based on defoliation studies conducted after flowering, Sideris and Krauss (1936) concluded that stem starch reserves were relatively unimportant for fruit filling or for sucker development. However, at high plant population densities and where relatively small plants are forced, starch reserves clearly have an important

role to play. Circumstantial evidence indicates that the continued development of axillary buds into suckers large enough to bear a ratoon fruit is determined by at least the presence, and perhaps the quantity, of stem starch reserves. The cultural practices that will delay sucker development include high plant population densities, forcing of small plants with minimal stem starch reserves, forcing during the summer, which produces relatively large numbers of fruitlets that must be filled in winter when irradiance is low, and forcing in warm humid climates, where net assimilation is low. The environmental factors that will delay sucker development are those that reduce plant net assimilation rates. These include warm night temperature, excessive day temperatures, low sunlight and stress associated with drought, nutrient deficiencies and pests and diseases.

To ensure a good ratoon crop, growers need to keep the root system healthy and provide optimum resources, while minimizing pest pressures. Anything that reduces plant net assimilation rates below the optimum will have an adverse effect on either ratoon sucker growth or fruit yield, or both.

Factors Influencing Fruit Quality during Development

Fruit quality in pineapple is subjective, because consumer preferences vary. However, the generally accepted factors influencing quality include fibrousness, porosity, colour, opaqueness, translucency, acidity, sugar, esters, aroma and taste (Sideris and Krauss, 1933b). Superior-quality fruit have a high TSS content and relatively low titratable acidity (TA), usually less than 1% as citric acid. However, low acidity can also lower quality (Sideris and Krauss, 1933a), as the fruit will be too bland, at least for those consumers used to fruit with higher levels of acid. Other measures of quality include the incidence of black heart, a postharvest disorder in some months in southern Queensland, Australia, an assortment of blemishes caused by insects and fungi (see Rohrbach and Johnson, Chapter 9, this volume) and nitrate levels (see Hepton, Chapter 6, and Malézieux and Bartholomew, Chapter 7, this volume), where fruit is destined for the cannery.

Irradiance and temperature

Mutual shading associated with higher planting densities decreased the proportion of translucent fruits and fruit specific gravity (Pinon, 1981; E. Malézieux, 1992, unpublished results). While shading materials or reflectant coatings can protect against fruit sunburn (Py *et al.*, 1987; Swete Kelly and Bartholomew, 1993), complete shading can reduce TSS (Py *et al.*, 1987), thus reducing fruit quality.

Irradiance or temperature or both are correlated with some compositional changes in the fruit. Relatively short-term effects have been observed with respect to malic and ascorbic acid. Over a 100-day sampling period that ended at maturity, the percentage of malate in fruit was inversely related to weekly pan evaporation for the week prior to sample collection. It was assumed that the changes in malic acid were associated with irradiance, since pan evaporation is highly correlated with irradiance (Gortner, 1963). Ascorbic acid content fluctuated in concert with daily irradiance, though the peak ascorbate level lagged the peak irradiance by about 2 weeks (Singleton and Gortner, 1965). It is not known whether the effects of irradiance on ascorbate or malate impact fruit quality at maturity in any way.

Changes in irradiance can apparently affect fruit TSS and TA, but there have been few definitive studies, particularly since growth-regulator-induced flowering became a common practice. Sideris *et al.* (1936) reported that fruit specific gravity increased from 1.005 at 50% light to 1.034 at ambient levels. TSS in juice was unaffected by light level. Titratable acidity, expressed as citric acid, increased from 0.74 to 1.4% as light was decreased from ambient to 50% of ambient levels. Hamner and Nightingale (1946) reported that TSS was unaffected by 50% shade, but juice acidity as citrate increased from 0.79 for control fruit to 1.12% for fruit

that ripened in 50% light. The increased acidity was attributed to the effect of shade on fruit temperature rather than available light (Hamner and Nightingale, 1946).

Fruit TSS in Côte d'Ivoire was relatively unaffected by seasonal changes in irradiance during the final 30 days of fruit development. Fruit TA varied relatively more than TSS and levels were highly negatively correlated with irradiance (Fig. 8.11; Malézieux and Lacoeuilhe, 1991). 'Smooth Cayenne' fruit grown in Thailand, where average temperatures are high, have such low acid levels that citric acid must be added to the fruit to permit low-temperature processing.

In Hawaii, fruit TA as citric acid in 'Smooth Cayenne' fruit varies from a low of about 0.85% in fruit harvested in summer to as much as 1.25% for fruit harvested in the winter. This seasonal variation in TA makes 'Smooth Cayenne' fruit less suitable for winter fresh-fruit production because TA reaches levels that lower fruit eating quality. Data from a study of the effects of elevation and season on growth, yield and fruit quality of 'Smooth Cayenne' pineapple showed that TA varied relatively more over the year than did TSS. TSS was not correlated with irradiance during the 30 days prior to harvest and was only poorly correlated with minimum temperature for the same period (R^2 = 0.352, n = 12). Fruit TA was negatively correlated with irradiance and minimum temperature. Irradiance accounted for 52.5% of the variation (n = 12) in TA, while temperature accounted for a slightly greater 63.4%. The two weather variables together accounted for 70.9% of the variation in TA. Fruit TA increased with increasing plant density (Py *et al.*, 1973; Chadha *et al.*, 1974), presumably due to increased mutual shading at the higher planting densities.

In the absence of significant variation in environmental temperature, irradiance can clearly affect fruit TA. However, in the presence of temperature variation or where irradiance and temperature vary together, it is less clear which factor is more important.

Titratable acidity can also vary within a fruit in relation to exposure. Flesh TA under the skin was less in sunburned areas than in unaffected parts of the fruit (Teisson, 1979a). When only part of the fruit was painted black to reduce its albedo, TA was significantly less in the painted parts than in the remainder of the fruit (Teisson, 1979b).

A physiological disorder referred to as green-ripe fruit and characterized by yellow, translucent flesh and a green skin results from a disjunction between internal and external ripening processes (Py *et al.*, 1987). The green-ripe disorder generally begins in the part of

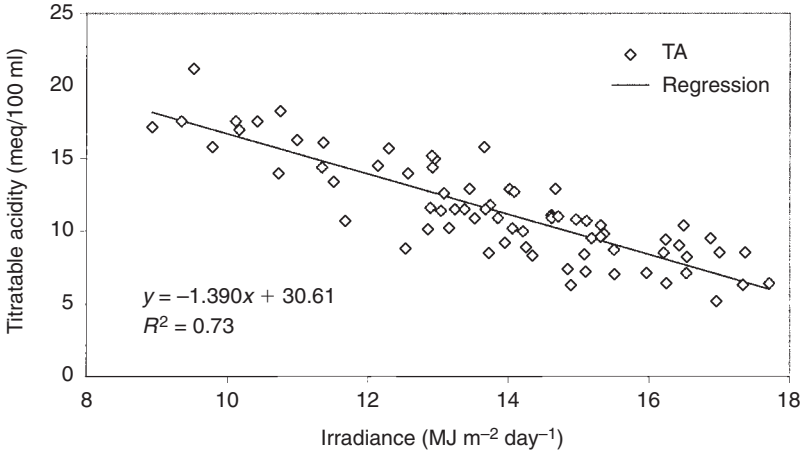

Fig. 8.11. Effect of mean irradiance for the 2 weeks prior to harvest on the titratble acidity (TA) of 'Smooth Cayenne' fruit juice. Data are means of 30 fruits harvested from 120 plantings made monthly in Côte d'Ivoire during a 10-year period.

the fruit exposed to the sun and the expression of the phenomenon decreases with shading (Teisson, 1979a). In a Côte d'Ivoire experiment, the percentage of green-ripe fruits decreased from 10% with no shade to 7 and 4% for partially and completely shaded fruits, respectively (Teisson, 1979a). The physiological basis for the effects of irradiance or increased temperature associated with irradiance, or both, on green-ripe fruit is not known.

Black heart, an internal browning of fruit flesh, is a common problem when pineapples are moved from refrigerated storage to room temperature (see Paull and Chen, Chapter 10, this volume). However, 'Smooth Cayenne' fruit that mature in southern Queensland during the cold winter months of July and August can develop black heart before harvest. Work by Wassman and Scott in 1972 (D. Christensen, 1999, personal communication) established a clear link between plant density, plant shading and the low-temperature inducement of black heart *in situ*. In their study, black heart increased from about 14% at a planting density of 24,700 plants ha^{-1} to 75% at 74,100 plants ha^{-1} and severity was much higher at the higher planting densities. Black heart does not occur in the field in 'Smooth Cayenne' in Hawaii.

Fruit become more translucent as the fruit ripen and air cavities in the fruit flesh become filled with juice. Fruit translucence increases from the base of the fruit to the top and translucent fruit were considered superior to opaque fruit for canning. However, as more pineapple are sold in the fresh market, translucency has come to be viewed as a disorder associated with preharvest development, because translucent fruit are more fragile and more prone to leak during storage and shipping than are opaque fruit. The incidence of fruit translucency varies with the season, being more prevalent in the spring in Hawaii than at other times of the year. Fruit also tend to become excessively translucent in Australia in spring, especially if heavy rain near fruit maturity follows dry conditions. The cause of the variation in fruit translucency is not known and growers experiencing this problem are interested in identifying cultural practices that will reduce its incidence and severity.

As fruit approach maturity, fruit sunburn discolours the shell and the underlying flesh becomes translucent and fragile (Py *et al.*, 1987) and, in extreme cases, the tissue desiccates and the injured portion of the fruit collapses. Ratoon fruit have a greater tendency to lodge than do fruit of the mother-plant crop, and lodging exposes the full length of the fruit cylinder to midday levels of irradiance (Swete Kelly and Bartholomew, 1993). This accounts for the observation that ratoon fruit are more susceptible to sunburn than plant-crop fruit. Sunburned fruit has reduced titratable acidity (Teisson, 1979b). In extreme cases, the exposed portions of both the shell and the underlying flesh are killed, the tissue dries out and the wound provides an entry point for disease organisms (Swete Kelly and Bartholomew, 1993). Fruit lying on their side have significantly higher temperatures than do upright fruit (Van Lelyveld, 1957; Gortner, 1960).

Gortner (1960) found that green-shelled fruits had a higher temperature than did yellow ones. Opaque and translucent fruits showed similar heating and cooling characteristics despite different internal air contents (Gortner, 1960). Spraying the fruit with water had a brief minor effect on the temperature beneath the shell but had no effect on the temperature at a 5 cm depth (Gortner, 1960). Shading the fruit with black, brown or white bags all reduced fruit temperature, relative to unshaded controls (Spiegelberg, 1960). Increasing the fruit albedo with white paint decreased fruit temperature while painting the fruit black had little effect on its temperature (Spiegelberg, 1960). By selection of the shading or coating material, a range in internal fruit temperature of more than 11°C could be obtained (Spiegelberg, 1960).

No data show that plant population density directly affects fruit quality. However, fruit harvest is delayed and fruit weight is more variable when high plant population densities are used.

Soil and nutrition

Nutrition, particularly potassium, can affect fruit quality. For details on the effects of

nutrition on fruit quality, see Malézieux and Bartholomew (Chapter 7, this volume).

Conclusions

Natural induction of flowering has been studied quite extensively, but the optimum conditions for induction are only known in a qualitative sense. With high-quality management practices, the incidence of natural induction tends to be low. However, in some years, for unknown reasons a high percentage of natural induction occurs. It would be valuable to identify the optimum conditions for natural induction because such knowledge might allow prediction of both the occurrence and incidence of natural induction. Such knowledge would allow for more rapid progress to be made on the control of natural induction with growth regulators and perhaps speed research on plants genetically engineered to control flowering. Plants presumably transformed to reduce their sensitivity to natural induction must be tested in conditions that promote natural induction. In the absence of precise knowledge about such conditions, a best estimate must be made.

As more areas shift to year-round production of pineapple to supply the fresh market, gaps in knowledge of the effects of seasonal variation in irradiance and temperature on ratoon-sucker development, plant sensitivity to forcing and fruit productivity and quality have become evident. Net assimilation and accumulation of storage reserves clearly affect all of the foregoing factors, but little research has been done on these topics. Funding of basic research on pineapple has almost never been a high priority in government-funded research organizations and, in the present funding climate, such research is unlikely to receive support. Basic research has typically not been done by growers, as their studies focus almost exclusively on site-specific research that seeks to optimize conditions for production within a given environment, is not published and often is not shared with other small or large growers. We see little chance for change, given the present competitive climate in the pineapple industry.

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9 Pests, Diseases and Weeds

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Introduction

Several recent in-depth reviews of pineapple pests and diseases have been published (Lim, 1985; Rohrbach and Apt, 1986; Broadley *et al*. 1993; Rohrbach and Schmitt, 1994). The focus of this chapter is on the interactions of populations of pineapple pests, disease pathogens and weeds with the pineapple production cycle. High population densities of pineapple pests, diseases and weeds occur at different times in the pineapple life cycle (shown by varying bar intensity for each insect and disease pathogen in Figs 9.1, 9.2 and 9.3), and therefore have varying impacts. Understanding the interactions of these pests and disease pathogens with their pineapple host is critical to an integrated pest, disease and weed management (IPM) programme.

Several characteristics of the pineapple plant and commercial pineapple production systems contribute to the severity of several pest and disease problems. The commercialization of pineapple required large capital investments in land and processing facilities, which has resulted in long-term monoculture. Long-term monoculture has contributed to severe nematode problems in many production areas and this has required the implementation of nematode-control strategies.

The pineapple plant is most productive under a xerophytic environment where low rainfall is supplemented by irrigation in well-drained soils. The adventitious roots arising from the lower portion of the pineapple stem are the only ones that become soil roots. Once the root system is damaged or destroyed, it does not regenerate significantly.

Indices for pineapple-plant diseases are the proportion of the plant population affected (incidence) and the effect of disease on each plant (severity). Severity may range from a reduction in growth rate, as indicated by a reduced plant size or weight, to a reduced fruit yield. Pineapple pest indices applicable to IPM systems have been developed for mealybugs, ants and mites.

In order to understand the epidemiology of pineapple-plant diseases and to develop management strategies, the probability of disease occurrence (frequency) and the level of disease occurring (incidence and severity) must be considered. Indices for fruit disease severity are shown in Figs 9.4 and 9.5. Factors of importance are the presence or absence of the causal organism, susceptibility of cultivars and optimum environmental conditions.

Fallow Period (Intercycle)

Intercycle pests

Nematodes, mealybugs and ants

In a monoculture pineapple production system, the fallow period or intercycle has historically ranged from years to as little as a

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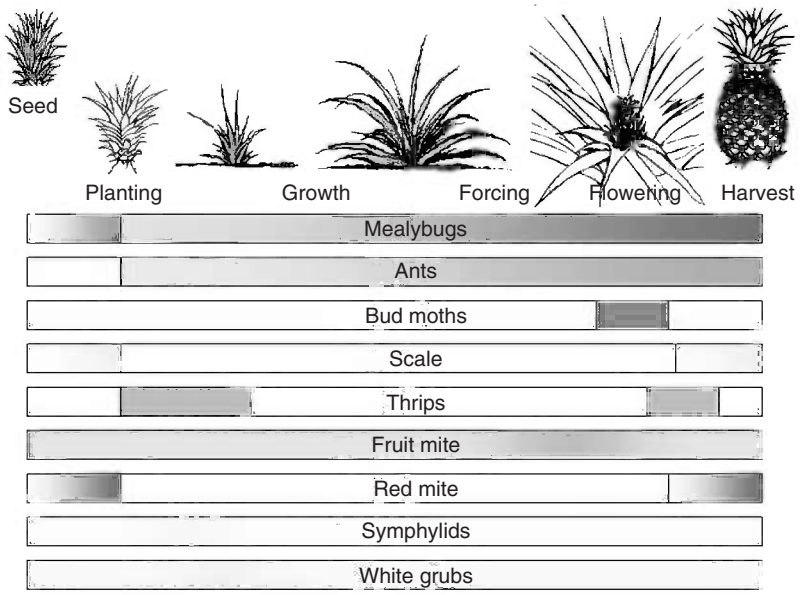

Fig. 9.1. Illustration showing typical frequencies of infestation of the most significant pineapple pests in relation to a plant-crop pineapple cycle. Darker area indicates higher frequencies.

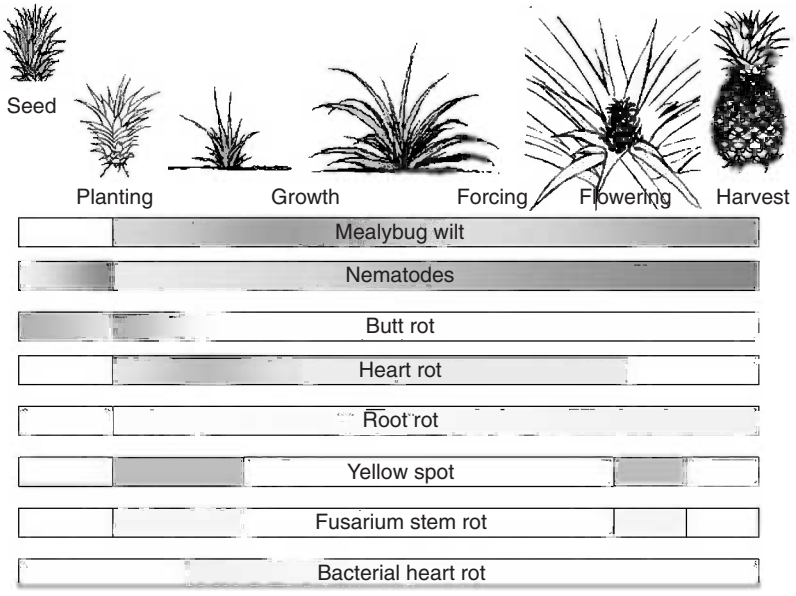

Fig. 9.2. Illustration showing typical disease intensities of the most significant pineapple diseases in relation to a plant-crop pineapple cycle. Darker areas indicate higher intensities.

few weeks. Prior to the discovery of soil fumigants for nematode control, the fallow period was an important nematode-control strategy, particularly for the root-knot nematode. The fallow period is also important for the control of ants and mealybugs which are associated with mealybug wilt. Tillage must be thorough and frequent enough for the decomposition of the previous crop and its pests and for the elimination of weed growth

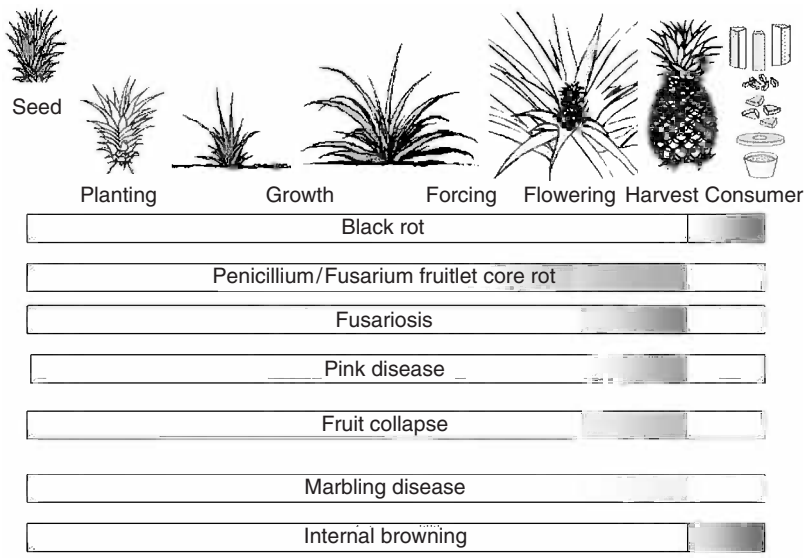

Fig. 9.3. Illustration showing typical pineapple fruit disease intensities of the most significant pineapple fruit diseases in relation to a plant-crop pineapple cycle. Darker areas indicate higher intensities.

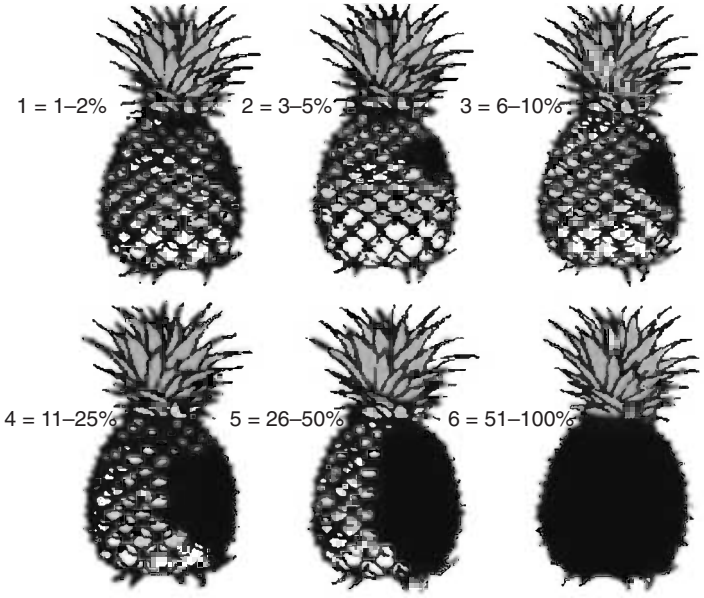

Fig. 9.4. Pineapple disease index used to measure external disease severity (e.g. black rot) based on the proportion of fruitlets per fruit that show symptoms.

during the fallow period. Weeds present during the fallow period may provide a carry-over host for nematodes and mealybugs. Thorough tillage can also eliminate ants within the fallowed field.

Ants present in intercycle fields are the big-headed ant, *Pheidole megacephala* (F.) (Plate 22), the Argentine ant, *Iridomyrmex humilis* (Mayer), and the fire ant, *Solenopsis geminata* (F.) (Rohrbach and Schmitt, 1994).

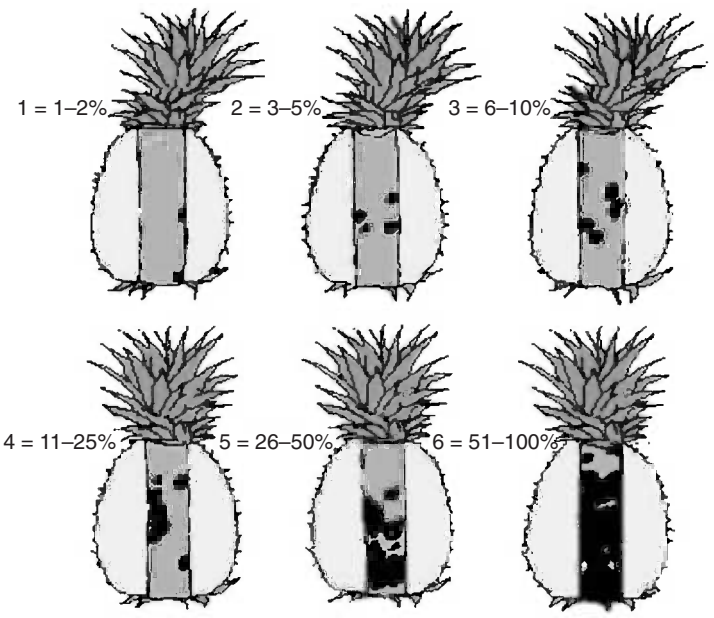

Fig. 9.5. Pineapple disease index used to measure internal disease severity (e.g. internal browning) based on the proportion of fruitlets per fruit that show symptoms.

With deep, frequent intercycle tillage, most ant colonies can be eliminated.

Nematode populations during the fallow period will decline significantly if soil moisture is adequate. However, the presence of soil moisture increases the need for weed control. Dry fallow is not as effective at reducing the reniform nematode population as is wet fallow (Caswell and Apt, 1989).

Economic thresholds for nematodes are not well defined. Soil sampling is important because the qualitative occurrence of reniform, root-knot or root-lesion nematodes is generally interpreted as a potential problem that requires control (Caswell *et al*., 1990; Stirling and Kopittke, 2000).

Souring beetles

Small nitidulid beetles (*c*. 4.5–8.0 mm), known as souring beetles, sap beetles or dried-fruit beetles, are attracted to decomposing pineapple plant material (termed pineapple trash) following knock-down of the previous crop. The adult beetles are hard-bodied and dark brown (Hinton, 1945). Several different species may infest trash or overripe pineapple fruit, of which *Carpophilus humeralis* (F.), *Carpophilus hemipterus* (L.) (Fig. 9.6), and *Haptoncus ocularis* (Fairm) are the most common (Carter, 1967; Py *et al*., 1987). Fertile females may lay more than 1400 eggs and live as many as 115 days (Carter, 1967). Eggs usually hatch within 2 days after deposition. Hinton (1945) indicates that the life cycle of *C. humeralis* from egg to adult is about 21 days. While the larvae typically feed on decaying fruit, the adults may attack pineapple plants at every stage of growth (Hinton, 1945). They may congregate on seed plants placed in the field and feed on the exposed butts and starchy stalk material. However, the injury to the plant is not economically significant. Chang and Jensen (1974) have identified these beetles as being possible vectors of the fungus *Chalara paradoxa* (De Seynes) Sacc. (syn. *Thielaviopsis paradoxa* (De Seyn.) Hohn) (telemorph *Ceratocystis paradoxa* (Dade) C. Moreau) which causes black-rot disease.

Souring beetles are more of a social nuisance than an agricultural one, because they

Fig. 9.6. Souring beetle, *Carpophilus hemipterus* L.

often land on humans in the vicinity of knocked-down fields and fruiting pineapple plantings. This has been a problem in places such as Hawaii, where recreational and tourist activities (e.g. golf) are enjoyed near pineapple-production areas. It has been reported (R. Heu, personal communication) that a single Maui resort company lost $50,000 weekly due to problems stemming from swarms of adult souring beetles. Given that these beetles do not have a significant impact on pineapple production, it is not economically feasible or environmentally desirable to control them with pesticides. However, to reduce their nuisance factor, the parasitic wasp *Cerchysiella* (= *Zeteticontus*) *utilis* Noyes (Hymenoptera: Encyrtidae) was collected in Israel and released in Hawaii in 1977 to control the immature larval stages of the beetles that infest rotting pineapple trash and fruit (Funasaki *et al*., 1988). The wasp established populations on the Hawaiian Islands of Oahu, Maui and Lanai (C. Nagamine, personal communication). The adult female parasitoid deposits her eggs into beetle larvae and the parasitized larvae mummify (i.e. turn hard and stiff) after 9–11 days. Fifteen days after egg deposition, an adult *C. utilis* emerges from the parasitized beetle. Souring-beetle numbers have been reduced somewhat, but the beetles still remain a problem in some areas.

Intercycle cover crops

While intercycle cover crops have not been utilized to any degree in commercial pineapple production, they offer some potential for controlling erosion and reducing nematodes (Ko and Schmitt, 1993). Their use has been uneconomic because adequate rainfall or irrigation is necessary to sustain cover crops in dry production areas.

Seed Material – Collection, Handling and Storage

Pineapple is vegetatively propagated, utilizing crowns, slips or suckers (Fig. 9.7). In general, these 'seed materials' are infested with the same pests as were present on the mother plants. The movement of seed materials from field to field or country to country has been the primary means of spread of the major pineapple pests and diseases (Rohrbach, 1983). Common pests infesting seed materials are mealybugs, scale and pineapple red mites. In addition to these pests, the diseases termed butt rot and *Fusarium* stem rot may be major problems when handling, storing or planting fresh seed materials. In the past 10 years, two types of plant viruses have been identified in pineapple, a closterovirus and a bacilliform

Fig. 9.7. Cross-section of a crown, slip and sucker used as 'seed materials' for pineapple propagation.

(Gunasinghe and German, 1989; Thomson *et al*., 1996). These viruses have been shown to occur in most pineapple plants with or without symptoms of mealybug wilt in several different countries (Sether and Hu, 1998). Recent evidence indicates that the closterovirus may actually consist of a group of viruses (J. Hu, personal communication). The role of these viruses in mealybug wilt has not been conclusively defined. Pest- and disease-free seed materials are critical to maintaining uniform and optimum plant growth throughout the pineapple cycle.

Mealybugs

The mealybug species associated with mealybug wilt are commonly found on pineapple seed material in most major production areas of the world. In order of importance worldwide, they are: pink pineapple mealybug, *Dysmicoccus brevipes* (Cockerell) (Plate 23), grey pineapple mealybug, *Dysmicoccus neobrevipes* Beardsley (Plate 23), and long-tailed mealybug, *Pseudococcus adonidum* (L.) (= *Pseudococcus longispinus* (Targioni-Tozzetti)). Insufficient mealybug control can lead to whole pineapple plantings being lost due to mealybug wilt, resulting in lost fruit production (Carter, 1933). The most common species found in Hawaii's pineapple plantings are *D. brevipes* and *D. neobrevipes*. Plantings may be infested with only one mealybug species or multiple species (Gonzalez-Hernandez *et al*., 1999). These species are not equally distributed worldwide. The pink pineapple mealybug may be found in all major pineapple-growing areas. In contrast, the grey pineapple mealybug has not been reported on pineapple in Africa, Australia, India, most of south Asia (except Thailand (G. Jahn, personal communication)), or the Mediterranean region (Beardsley, 1993).

The pink pineapple mealybug is commonly found on the lateral roots of the pineapple plant just below soil level. It can also be found on the aerial parts of the plant, mainly in the leaf axils and on the developing fruit. In contrast, the grey pineapple mealybug is never found on the pineapple roots, but may overlap the distribution of the pink pineapple mealybug on the aerial portions of the plant. In Hawaii, only the grey pineapple mealybug has both female and male individuals in the population, while the pink pineapple mealybug only has females. The male grey pineapple mealybugs spin white, silky cocoons before becoming small-winged insects, which seek females to mate. Mealybugs feed on plant sap in the phloem of their host plants. They produce honeydew (sweet, sticky liquid) as a by-product of their feeding. The honeydew often accumulates in large quantities around groups of mealybugs and may support the growth of sooty mould, *Capnodium* sp. Adult mealybugs are elliptical-shaped (top view), soft-skinned insects with waxy secretions, which give their body surfaces a chalky appearance. They also have white, waxy filaments of various lengths (depending on the species) extending from the lateral margins of their bodies. Although capable of movement, these insects are normally quiescent and congregate together in groups (e.g. > 20 individuals). The first-stage (or first-instar) crawlers (0.6–0.7 mm) are typically the most active stage, and they

move around the plant host seeking a place to settle down to feed. After settling down, they do not normally move any great distance, unless disturbed or relocated by ant species (e.g. big-headed ant) that tend them for their honeydew.

The long-tailed mealybug and the citrus mealybug, *Pseudococcus citri* (Risso), may be found on pineapple, but do not cause significant injury. The adult of the former species has long filaments protruding from its posterior end, these are slightly longer than the length of the mealybug's body. The immature stages of the citrus mealybug are similar in appearance to immature pink pineapple mealybugs, but the adult stage produces a fluffy wax mass which holds its golden-coloured eggs.

Scale

The pineapple scale, *Diaspis bromeliea* (Kerner), is likely to be found on pineapple leaves and fruit worldwide (Plate 24) (Waite, 1993). Frequently, it builds up on the crown of the developing fruit and, at harvest, the seed material may be heavily infested. Other hosts likely to be found in areas where pineapple is grown include species of *Agave*, *Billbergia* and *Bromelia* (Petty, 1978b). Unlike mealybugs, the immature and adult female stages of scale insects do not move around except in the crawler stage, which is responsible for dispersal of the insect (Beardsley and Gonzales, 1975). Adult male scales have wings but fly only to locate females for mating. The crawlers commonly disperse by active wandering and wind currents. The newly hatched crawlers emerge from underneath the protective scale covering of their mothers.

Seed material should be as clean as possible, because scale densities can increase to high numbers (especially if infested planting material is piled up) and desiccate the planting material, thereby making it unusable (Waite, 1993).

Butt rot

Butt rot or 'top rot' of pineapple can be serious on pineapple 'seed materials' and occurs wherever pineapple is grown (Rohrbach, 1983). The causal fungus, *C. paradoxa,* is widespread in the tropics on pineapple, coconut and other palms, sugar cane as 'pineapple disease', cacao as 'pod rot', and banana as 'black-head disease' on rhizomes, suckers and roots, and as 'stem-end rot' on fruit (Dade, 1928).

The symptoms of butt rot are a soft rot and blackening of the basal portion of the stem tissue of vegetative seed material (Fig. 9.8). If infected seed material is kept wet, as in a pile of crowns, the infection may progress to rot the entire seed piece (stem and leaves) or even the entire pile. Severely rotted seed material is normally discarded prior to planting. Slightly to moderately infected seed material may be planted, but growth will be slow and plants will be stunted, due to loss of stem tissue, which contains carbohydrate reserves and the initial roots.

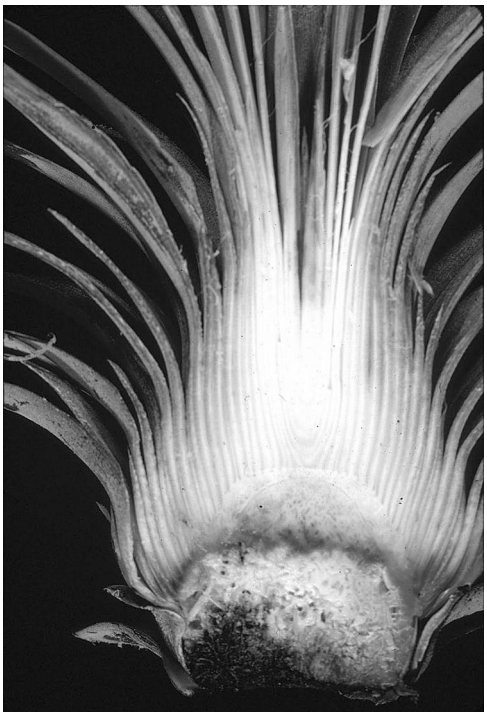

Fig. 9.8. Cross-section of crown showing pineapple butt rot caused by *Chalara paradoxa* and the loss of tissues from which adventitious roots arise.

When uncured or untreated seed material is planted in soils with high inoculum levels of *C. paradoxa*, butt rot levels may reach 100%. Inoculum levels in pineapple soils in Hawaii varied from an average of 2630 propagules g^{-1} following field preparation to 280 propagules g^{-1} of soil at the end of the crop cycle. At planting, inoculum levels varied by field from a high of 12,969 to as low as 31 propagules g^{-1} of soil (Rashid, 1975).

Fusarium stem rot

Fusarium stem rot is caused by the fungus *Fusarium subglutinans* (Wollenw. & Reinking) Nelson, Tousson & Marasas comb. nov. (Matos, 1999). Recently, O'Donnell *et al*. (1998) renamed the pathogen *Fusarium guttiforme* Nirenberg & O'Donnell based on DNA sequence analyses of members of the *Gibberella fujikuroi* complex. Despite its obvious affinities with *G. fujikuroi*, no teleomorph has been reported for this pathogen.

In Brazil, the disease causes major losses in the three major cultivars, 'Perola', 'Jupi' and 'Smooth Cayenne' (Rohrbach, 1983). Levels of plant infections vary from 2 to 30% (Laville, 1980). Disease levels in commercial experimental 'Smooth Cayenne' plantings have been so high that foreign investments in pineapple production in Brazil have not developed, although attempts have been made (L. Cooksey, personal communication).

The disease is associated with the fruit-rot phase termed 'fusariosis'. Stem infections of seed materials occur at leaf bases, with resulting rosetting and/or curvature of the plant, due to portions of the stem being girdled or killed (Fig. 9.9; Laville, 1980).

Once the developing fruit is infected, secondary infections can occur on the developing slips or suckers. The infected seed material is then distributed to new planting areas, thus infesting new sites. Soils can remain infested for several months. Spread within infested fields is primarily by insects but may also be by wind (Laville, 1980). Free conidia of *Fusarium subglutinans* can survive for 6–13 weeks in soil, depending on moisture and temperature, with survival being highest in dry soils. Survival in infected pineapple tissue in soil is less than 10 months (Maffia, 1980). Optimum temperatures for growth are 25°C, with a range of 5–35°C (Camargo and Camargo, 1974).

Mites

Several mite species have been recorded on pineapple worldwide. Because of this, some mites have more than one common name and some names have been applied to more than one mite species. To reduce the confusion in the discussion below, the various common names applied to each mite species have been provided.

The pineapple red mite (also known as red spider or false spider mite), *Dolichotetranychus* (= *Stigmacus*) *floridanus* (Banks) (Acarina: Tenuipalpidae), is the largest mite found on pineapple and is conspicuous *en masse* because of its bright orange to red colour (Fig. 9.10). According to Jeppson *et al*.

Fig. 9.9. Cross-section of a pineapple sucker showing *Fusarium* stem rot caused by *Fusarium subglutinans*.

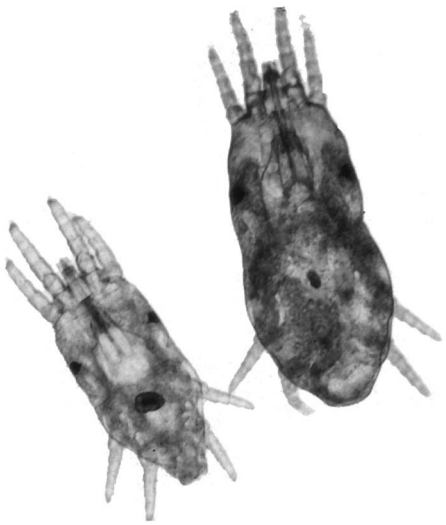

Fig. 9.10. The pineapple red mite, *Dolichotetranychus floridanus* (male left, female right).

(1975), it only occurs on pineapple and is found in Florida, Cuba, Puerto Rico, Panama, Honduras, Mexico, Central America, Hawaii, the Philippine Islands, Japan, Okinawa and Java. The adult mite is approximately 0.3–0.4 mm long and 0.1 mm wide. When present on the plant, the mite is always found on the white basal portion of the leaves, where it feeds, particularly on the crown. When pineapple red-mite populations build up under dry conditions, the mites are most commonly on the basal leaves of the crown and on stored seed material (Petty, 1975, 1978c).

The blister mite (also called pineapple fruit mite), *Phyllocoptruta* (= *Vasates*) *sakimurae* Kiefer (Acarina: Eriophyidae), is reportedly the smallest mite (0.1 mm long and 0.033 mm wide) found on pineapple in Hawaii (Carter, 1967). Individuals are chalky in colour and only have two pairs of legs located near the head. They may be found on detached crowns that are stored for planting. They originate from prior infestations on the ripe fruit from which the crowns were derived. They normally disappear after the crowns are planted, but may be found later on fruit after the flat-eye stage of fruit development (Carter, 1967). Jeppson *et al.* (1975) suggest that the mite originated in South America.

The pineapple mite, *Schizotetranychus asparagi* (Oudemans) (Acarina: Tetranychidae), is widely distributed and has been recorded in Hawaii, continental USA, Germany, Portugal, The Netherlands and Puerto Rico (Jeppson *et al.*, 1975). In colder climates, it may be found on asparagus ferns grown in greenhouses or lathhouses. In pineapple-production areas, it may frequently cause severe damage to recently established plants in the field. Plants that are infested in the early stages remain small and fruit production is either curtailed or non-existent. Heavily infested plants may die before producing fruit. The best management action is to plant only mite-free seed-plant material (Jeppson *et al.*, 1975).

The pineapple tarsonemid mite (also known as pineapple mite, pineapple fruit mite, pineapple false spider mite), *Steneotarsonemus ananas* (Tryon) (Acarina: Tarsonemidae), may be found infesting pineapple later in the plant's phenological cycle (see discussion below) (Fig. 9.11).

Management of pests and diseases on seed material

Pest- and disease-free seed materials are critical to preventing the establishment of insects and pathogens in newly planted pineapple fields. The presence of mealybugs, scales and mites, as well as *Fusarium*-infected seed materials, must be monitored at the seed source before transport for planting, in order to implement effective controls. The pineapple red mite (*D. floridanus*) will only become a problem on stored seed under dry conditions. Mealybugs, scales and the red mite can be controlled by dipping seed in an approved insecticide, such as diazinon (Petty and Webster, 1979). Red mites can also be controlled by orientating seed material in its normal vertical position, so that the leaf axils collect natural rainfall or dew, or by methyl bromide fumigation of the seed material (Osburn, 1945). The blister mite (*P. sakimurae*) can be controlled by dipping seed materials in an approved miticide, such as endosulphan.

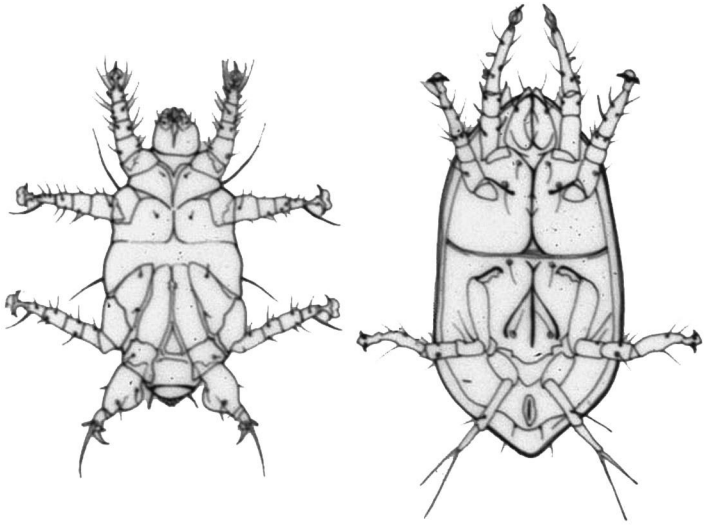

Fig. 9.11. Illustration of the pineapple tarsonemid mite, *Steneotarsonemus ananas* (male left, female right).

Fusarium-infected seed has been hot-water-treated at 54°C for 90 min with benomyl at 50 g 100 l^{-1}, but growth was retarded and up to 50% of the plants were killed (Maffia, 1980). Resistance to *F. subglutinans* occurs in *Ananas* and *Pseudoananas* (Laville, 1980). Resistant cultivars are being developed (Cabral *et al.*, 1997).

Butt rot is controlled by harvesting seed material during dry weather and curing it on the mother plants, where there is good air circulation and exposure to inoculum-infested soil is minimized (Fig. 9.12). Where mechanization has permitted immediate planting of freshly removed seed material, thus eliminating the time required for

Fig. 9.12. Curing (drying) 'seed material' (crowns) on the mother plants and storage until collected for planting.

Fig. 9.13. Pineapple dipping equipment for treating seed materials with fungicides for butt-rot control or insecticides to control scale or mealybugs.

curing, seed must be dipped in an approved fungicide, such as benomyl or triadimefone within 12 h of removal from the fruit or, in the case of slips, from the plant (Fig. 9.13; Rohrbach and Schmitt, 1994).

Cultivars vary in susceptibility to butt rot with the 'Red Spanish' types being more resistant than 'Smooth Cayenne' (Smoot *et al*., 1971). Hybrid cultivars have also shown a wide range of susceptibility (K.G. Rohrbach, unpublished results).

The strong association of a complex of at least two closteroviruses with pineapple mealybug wilt indicates that virus-free seed may be important for wilt control (Sether and Hu, 1998; Melzer *et al*., 2001). Elimination of the virus from pineapple plants has been attempted with heat treatments (Ullman *et al*., 1991, 1993). Tissue-culture techniques have eliminated virus infection (Sether *et al*., 2001). Genetic engineering for virus resistance is also being attempted (Rohrbach *et al*., 2000).

Some pineapple insects and disease organisms may become quarantine issues if seed materials are transported between countries or production areas where pest organisms are present and areas where they are not established. With the increasing importance of low-acid, fresh-fruit cultivars for niche fresh-fruit markets, the potential for international movement of seed materials presents some significant quarantine issues, when specific pests and diseases are not established in the importing country. Potential quarantine insects and diseases because of limited distribution are the pineapple bud moth, *Thecla basilides* (Geyer), from Central America and the pineapple stem borers from South America and the Caribbean (*Castnia icarus* (Cramer), *Metamasius ritchiei* (Marshall) and *Paradiophorus crenatus* (Billberg)), *Erwinia chrysanthemi* (Burkholder *et al*.), causing bacterial heart rot, and *F. subglutinans* from South America, causing stem and fruit rot. Seed materials originating in areas where these pests and diseases are reported to occur should be excluded from areas where they are not established or should be quarantined before planting in production areas (Rohrbach, 1983).

Planting and Early Growth (First 3 Months)

Uniformity of early growth is critical to uniform forcing and harvest. Incipient butt-rot infections may severely affect early plant-growth uniformity (Plate 25). Depending on initial populations of root pathogens at planting and the soil environment, nematodes, symphylids and root-rot pathogens may begin to attack the newly developing root system by the end of the first 3 months of growth. Seed material infested with mealybugs and/or scale at planting provides a source of pests that only requires ants to begin to establish damaging mealybug populations throughout the field and the potential for development of mealybug wilt. Additionally, during early growth, plants are especially susceptible to the fungal and bacterial heart rots.

Above-ground symptoms of potential root health problems will not generally be evident during early plant growth. However,

nematode populations will begin to increase. Ants, if uncontrolled, will begin to move into the field from adjacent areas or from in-field colonies that were not destroyed by fallowing practices and will begin to expand. With increases in ant infestation, mealybugs will increase and, if uncontrolled, will have the potential to cause mealybug wilt.

The above-ground symptoms of root rot are similar to any symptom resulting from loss of a functional root system (e.g. mealybug wilt, nematodes, symphylids, root rot and water stress). Infected plants are stunted, show signs of stress and may or may not be easily pulled out of the soil. Thus, symptoms must be associated with evidence of poor soil drainage for fungal root rot, nematode galls for the root-knot nematode, and ants and mealybugs for mealybug wilt. Soil and root sampling for nematodes should be done to confirm their presence during this period.

Weeds

Weed management in pineapple is especially important during early growth, because weeds compete for water, nutrients and light, are hosts for pineapple pests and viruses and interfere with production operations. Weed management includes soil tillage, mulches, and the use of pre-emergence (applied prior to weed-seed germination) and post-emergence herbicides (Fig. 9.14; Kasasian, 1971; Glennie, 1991). The efficiency of the pineapple weed-management system is affected by plant density, the degree of mulch cover, soil type and natural rainfall and/or the method of irrigation. Because the pineapple plant is relatively slow in establishing a complete ground cover, eliminating weed cover may result in high levels of soil erosion (El-Swaify *et al.*, 1993).

Prior to the introduction of pre-emergence herbicides in the 1950s, weed management was primarily physical removal by tillage. The introduction of pre-emergence herbicides revolutionized weed control in pineapple, particularly the grasses. In general, the perennial grasses are much more difficult to control than the broad-leaved weeds. Important pineapple herbicides have been diuron, bromacil, amytryn, atrazine and paraquat (Glennie, 1991). No one herbicide will control all weeds in all situations.

Fig. 9.14. Application of pre-emergence herbicide or postplant nematocides or fungicides to young pineapple plants.

Each production area has its own particular spectrum of weeds, sometimes determined by historical weed-control practices (St. John and Hosaka, 1932; Barbier and Trapin, 1956; Py, 1959; Silvy, 1962), e.g. wild sugar cane (*Saccharum spontaneum* L.) in the Philippines (Sison and Mendoza, 1993). Species that are particularly difficult to manage are *Panicum maximum* var. *maximum*, *Sorghum halepense* and the paspalums, *Paspalum dilatatum* and *Paspalum urvillei*. The sedge *Cyperus rotundus* (nut grass) is also a serious pest. Significant broad-leaved weeds are the morning glories, *Ipomoea cairica*, *Ipomola plebeia*, *Ipomola indica*, *Ipomola purpurea* and *Ipomola triloba*. Perennial weeds (e.g. *S. spontaneum*, *S. halepense*, *Imperata cylindrica*) are destroyed by deep ploughing.

Pre-emergence herbicides are used most commonly in pineapple production. Effectiveness is dependent on proper seed-bed preparation, including no live weeds, adequate soil moisture, complete soil coverage and no subsequent soil disturbance following application (Dalldorf, 1985). Split applications of pre-emergence herbicides may be made to pre-mulched or mulched and postplanted fields to ensure adequate pre-emergence protection through the preplanting/planting period. Weed 'escapes' during the first crop are controlled with bromacil at 2–4 kg ha^{-1} or dalapon at 6–10 kg ha^{-1}. *C. rotundus* and *Panicum repens* appearing in the next cropping cycle are controlled with bromacil at 2–4 and 10 kg ha^{-1}, respectively. Other weeds (*I. triloba*, *Mimosa invisa*, *Crotalaria mucronata*, *Digitaria sanguinalis*, *Eleusine indica*, *Paspalum conjugatum*) are controlled by pre-emergence sprays of bromacil at 1–2 kg ha^{-1}, diuron at 0.75–1.5 kg ha^{-1}, ametryne or atrazine (Mendoza, 1979). A summary weed-control programme is identified for Brazil (Reinhardt and Cunha, 1999).

Once plants begin to grow, herbicide applications should be directed away from the plants and on to the soil and developing weeds. This is particularly true with herbicides such as bromacil (Dalldorf, 1985).

Grasses

Preventing grasses from producing seed both in the field and on field borders is critical to economically effective weed management. The adage of '1 year's seeding means 7 years' weeding' holds true (Broadley *et al*., 1993).

Broad-leaved weeds

In contrast to grasses, broad-leaf weeds are relatively easy to control. However, some broad-leaved weeds, such as *Emilia sagittata*, may cause secondary damage in low population densities as alternative hosts for the yellow-spot virus.

Nematodes

Four species of nematodes have been associated most frequently with, and caused the most damage to, pineapple: the root-knot nematodes, *Meloidogyne javanica* ((Treub) Chitwood) and *Meloidogyne incognita* ((Kofoid & White) Chitwood), the reniform nematode, *Rotylenchulus reniformis* (Linford & Oliveira) and the root-lesion nematode, *Pratylenchus brachyurus* (Godfrey Filipjev & Schuurmans Stekhoven) (Caswell *et al*., 1990).

Root-knot nematodes

The most obvious symptom of root-knot nematodes, *M. javanica* and *M. incognita*, on pineapple is the terminal club-shaped gall resulting from infection of the root tip (Fig. 9.15). Less obvious symptoms include stunting of plants and water stress, with the terminally galled root resulting in poor plant anchorage. Nematode egg masses survive for relatively short periods (hours) in desiccated soils. Egg masses in galls may survive several days. Juveniles may survive several weeks to years in desiccated soils. Second-stage juveniles infect the pineapple root tip and become sedentary after 2–3 days. Vermiform males and saccate, sedentary females go through several moults. Surviving nematodes can tolerate a wide range of soil temperatures and pH.

Reniform nematode

The reniform nematode, like the root-knot nematode, causes stunting of plant growth,

Fig. 9.15. Root-knot nematode galls on pineapple roots caused by *Meloidogyne javanica*.

with infected plants appearing to be under water stress, much the same as in drought, mealybug wilt or root rot. Symptoms are most severe in ratoon crops and may result in the total collapse and death of the plants. As with root-knot, above-ground symptoms are not diagnostic. In contrast to root-knot, however, pineapple plants infected with the reniform nematode have excellent anchorage because of the lack of terminal galling. Infected primary roots continue to grow but secondary root growth is severely limited. Infected roots appear to have nodules, which are actually soil clinging to the gelatinous matrix of females embedded in the roots (Fig. 9.16; Caswell and Apt, 1989). Reniform nematode eggs hatch when stimulated by root exudates of host plants. Second-stage juveniles in the soil undergo 3 moults without feeding, ending as either adult males or preadult females. The preadult females infect the root, where they establish sedentary feeding, become swollen mature adults and start producing eggs. The male does not feed.

Root-lesion nematode

The infection sites of the root-lesion nematode, *P. brachyurus*, are characterized by a black lesion that progresses along the root as the nematodes move for feeding. Secondary roots and root hairs are also destroyed. Initial inoculum comes from infested root fragments in the soil or infected roots on infested seed material. Once the plant is infected, the entire life cycle can be completed within the pineapple root. Reproduction is by mitotic parthenogenesis, with males being rare. Optimum soil temperatures are 25–30°C and populations do best in acid soils. In the highly acid Ivory Coast soils, the root-lesion nematode displaces the root-knot nematode. A combination of root-lesion nematode and *Pythium* species results in greater damage than either alone (Guerout, 1975).

Other nematodes

Spiral nematodes – *Helicotylenchus*, *Scutellonema* and *Rotylenchus* spp., have been reported as problematic in South Africa (Keetch and Purdon, 1979). In Bahia, Brazil, *Aorolaimus* spp. have been reported to cause stunting (Costa *et al*., 1998).

Ants and mealybugs

Mealybug wilt of pineapple, with its leaf-tip dieback and plant yellowing and reddening, is a symptom associated with the feeding of mealybugs (Plate 26). The actual cause has not been conclusively demonstrated, but one or two closteroviruses have been implicated (Sether and Hu, 1999). Mealybug wilt is a universal problem; the only exception may be in parts of Thailand, where wilt does not occur even though mealybugs are present. Mealybug wilt is clearly one of the most destructive diseases of pineapple plants, and field controls must be initiated during the fallow period and continued to harvest. High mealybug populations are required to cause wilt. Ants are necessary for populations of mealybugs to develop and reproduce in pineapple fields, where mealybug

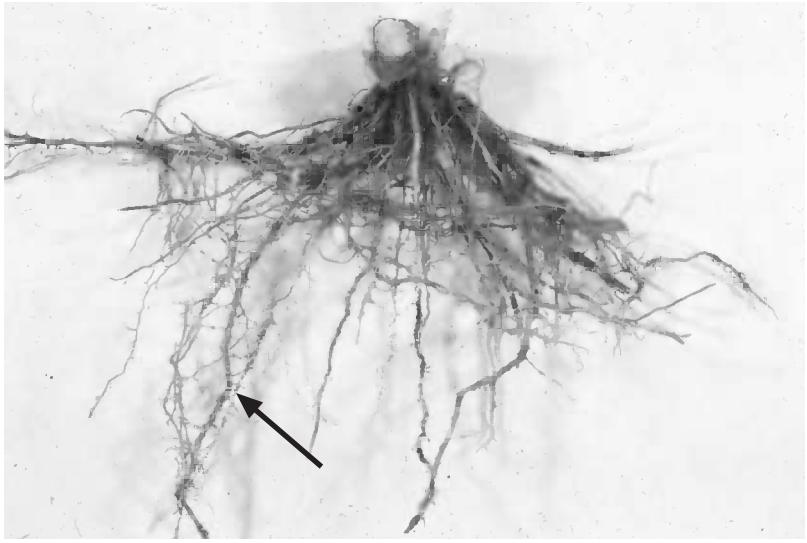

Fig. 9.16. Pineapple root system showing soil sticking to reniform nematode egg masses (arrow) and the lack of secondary roots.

parasitoids and predators are present. At least three species of ants are associated with mealybugs in Hawaii: the big-headed ant, the Argentine ant and the fire ant (Rohrbach and Schmitt, 1994). Two other species – the long-legged crazy ant, *Anoplolepis longipes* (Jardon), and the white-footed ant, *Technomyrmex albipes* (Fr. Smith) – are clearly associated with mealybugs in pineapple fields and, although not demonstrated to be associated with wilt, may have a role because they clearly tend mealybugs (G. Taniguchi, personal communication). The ant association with mealybugs involves protection from predation and parasitism, removal of excess honeydew, which increases mealybug mortality and movement of the mealybugs into new areas. Preventing the establishment of new ant colonies in new plantings is critical to preventing mealybug wilt (Rohrbach and Schmitt, 1994).

Symphylids

Symphylids are wingless, soil-inhabiting arthropods (6–10 mm in length), which are distantly related to insects. Whereas adult insects typically have six legs, symphylids have more than six legs in the adult stage (normally adults have 12 pairs of legs, with larvae having six or seven pairs) (Borror and De Long, 1971; Py *et al*., 1987). Symphylid adults are white, with relatively long antennae projecting from the head. Several species are found in pineapple plantings: *Hanseniella unguiculata* (Hansen), *Hanseniella ivorensis* Juberthie Jupeau and Kehe, *Scutigerella sakimurai* Scheller, and *Symphylella tenella* Scheller (Carter, 1967; Py *et al*., 1987; Waite, 1993). Previously, some species were misidentified as being pineapple pests: *Hanseniella caldaria* (Hansen) *Symphylella simplex* (Hansen), and *Scutigerella immaculata* (Newport) (Carter, 1967). Additionally, Carter reports that, in Hawaii, *S. tenella* is basically a scavenger, while *H. unguiculata* is a root feeder. *S. sakimurai* tends to be less common.

These organisms are blind, avoid the light, absorb water from their environment and typically move through the natural cracks and crevices found in soils (Py *et al*., 1987). Symphylids are only important in specific areas that are favourable to their reproduction and survival (Py *et al*., 1987). They proliferate in well-aerated soils with high organic-matter content. They are most

common in volcanic calcareous tufa or gravelly soils possessing a high percentage of clay. Easily compacted, sandy and clayey–sandy clay soils do not usually support large symphylid populations. Soil temperature influences daily movement of symphylids in the soil, whereas soil humidity affects seasonal migrations to more humid areas. These organisms may survive for up to 4 months without food if the humidity is suitable. They are also cannibalistic if their preferred foods are absent.

Those symphylids that are important pineapple pests feed on plant root tips and hairs (Carter, 1963; Py *et al*., 1987). Injury from their feeding disturbs the roots' abilities to absorb nutritive elements, which depresses plant growth and development (Plate 27). Where they do damage crops, they can cause dramatic yield decreases (Lacoeuilhe, 1977; Kehe, 1979). They have their greatest impact where soil humidity is a limiting factor, and plants cannot recover from the inflicted injury even if symphylid feeding is curtailed.

Depending on the age of a plant, different effects will be observed from symphylid feeding on roots. Usually, younger roots in the meristem region are preferred. Feeding on these tissues can lead to the formation of a 'witches' broom' appearance in the roots (Kehe, 1979). Long-term feeding on the roots can make the root tips appear clublike. If feeding is intense on very young plants when roots are just emerging (within the first 2 months of planting), the roots will not grow more than a few centimetres. Where intense feeding occurs, roots will have a 'bushy' appearance around the stem base, have poor anchorage (an element of crop logging) (see page 144, Chapter 7, this volume) and not function efficiently (Kehe, 1980). Plants may lodge due to the lack of root support. Symphylids may also be problematic 4–5 months after planting when a second flush of roots appear (Kehe, 1979). Symphylid-inflicted injury to the roots may also provide entrance to 'wound' pathogens, which can destroy the root (Sakimura, 1966).

Approved insecticidal controls (e.g. lindane) applied at planting are the best management tool at present available for symphylids (Py *et al*., 1987). If an infestation is verified, action should be taken to reduce symphylid densities, especially when roots are flushing. Very dry and wet periods do limit symphylid growth, but at other times are suitable for reproduction and survival (Py *et al*., 1987).

White grubs

The white grubs (i.e. larval stage) of several beetle species in the family Scarabaeidae commonly infest the roots of pineapple plants. Scarab species reported feeding on pineapple roots include, in Australia: the southern one-year canegrub (also known as rugulose canegrub, nambour canegrub), *Antitrogus mussoni* (Blackburn), Christmas beetle, *Anoplognathus porosus* (Dalman), rhopaea canegrub, *Rhopaea magnicornis* Blackburn, squamulata canegrub, *Lepidiota squamulata* Waterhouse (= *Lepidiota darwini* Blackburn, *Lepidiota leai* Blackburn, *Lepidiota rugosipennis* Lea), noxia canegrub, *Lepidiota noxia* Britton, and *Lepidiota gibbifrons* Britton (Waite, 1993); in South Africa: *Adoretus ictericus* Burmeister, *Adoretus tessulatus* Burmeister, *Trochalus politus* Moser and *Macrophylla ciliata* Herbst; and in Hawaii: Chinese rose beetle, *Adoretus sinicus* Burmeister, and *Anomala* beetle, *Anomala orientalis* Waterhouse (Carter, 1967). The species *Heteronychus arator* (Fabricius) is found in Africa and Australia, where it is referred to by the common names black maize beetle (Petty, 1976a) and African black beetle (Waite, 1993), respectively. The species above vary in the levels of damage they cause to pineapple. Additional scarab species that attack pineapple may also exist in these areas and other locations where pineapple is grown. Scarabs are not limited to pineapple in their feeding habits and may attack a wide range of plants. The various species of beetles can be separated in both the larval and adult stages by morphological characters on the body (Carter, 1967; Petty, 1977a).

In most cases, adult scarabs do not significantly damage the pineapple plant, if at all. Many species do not feed on pineapple plants as adults. However, exceptions do

exist, such as the adult stage of *H. arator* which occurs in Australia, New Zealand and South Africa (Waite, 1993; Petty, 1977a) and bores into the lower stems of the pineapple plant. Adults of *A. sinicus* in Hawaii may riddle or completely destroy pineapple leaves, while the larvae rarely attack the roots (Carter, 1967). Fortunately, adult *A. sinicus* infestations are typically spotty in an area. On the other hand, adults of *A. orientalis* typically remain in the soil and lay their eggs in the vicinity of where they developed (Carter, 1967).

Adult scarab females are free-flying and choose the locations where they will lay their eggs in moist soil. Egg deposition preferences for soil conditions and type vary among scarab species (Waite, 1993). Eggs are oval in shape and, after hatching, the first-instar larvae feed on organic matter in the soil. Older scarab larvae develop within the soil among the roots of their host plants (e.g. pineapple). They feed upon organic matter within the soil as well. Although white grubs are not immobile, they do not disperse far from where the eggs were laid. White grubs are easily identified by their white or ivory-coloured, 'C'-shaped bodies, which are soft and plump. The posterior quarter to third of the larval abdomen is commonly a dark blue-grey colour, due to the contents of the digestive system. Grubs have three pairs of legs near their anterior end and a tan to dark brown head capsule (Waite, 1993). They may injure pineapple plants by: (i) feeding on the roots, which interferes with nutrient and water uptake and transport (Carter, 1967; Petty, 1978a; Waite, 1993); (ii) weakening or destroying the roots that anchor the plants in the soil (Waite, 1993); and (iii) wounding plant tissues, which enables secondary plant pathogens to enter the plant (Carter, 1967). If infestations are severe, a crop may be lost, especially in the ratoon crop (Waite, 1993). The length of the scarab developmental cycle varies among species and climatic conditions, but generally they grow slowly compared with most insect pests and may require 1–2 years to complete development to the adult stage (Waite, 1993).

Recognition of white-grub infestations is difficult until significant injury to pineapple plants becomes obvious, commonly in the ratoon crop (Waite, 1993). Plants may become stunted, wilted and chlorotic (Petty, 1978a). Severely affected plants are easy to pull out of the ground (Waite, 1993). Additionally, pathogens, such as *Pythium* fungus and root-knot nematode, may infect the plant (Carter, 1967). Areas designated for pineapple plantings should be inspected for the presence of white grubs prior to planting the seed crop. Larvae in the soil may be uncovered using a spade or found during cultivation of the soil (Waite, 1993). Adult beetles may be monitored using light traps (Petty, 1977a). Thorough cultivation of the soil will reduce white-grub populations. A preplant soil treatment with long-term residual activity is appropriate for areas where white grubs are historically a recurring problem (Waite, 1993). Given the long production cycle of pineapple (i.e. seed crop and ratoon crops), the long-term effectiveness of chemical soil treatments is limited. Discoveries of white-grub infestations after planting are problematic because of the difficulty in controlling them. Delivery of chemicals to the insects is a challenge. Natural enemies of these pests do exist (insect predators, parasitoids and pathogens, as well as birds, toads, wild pigs and rodents), but the levels of control are not typically adequate (Carter, 1967; Petty, 1976b). Petty (1976b) reviews other control methods, but none appear overly successful or practical.

Scales

Pineapple scale, *D. bromeliea*, varies in its impact on pineapple. In some places (e.g. Australia), it does not typically reduce fruit yield directly, but affects fruit appearance so that the value is reduced (Waite, 1993). In other places (e.g. Hawaii, South Africa, etc.), high scale densities kill plants (Carter, 1967; Petty, 1978b; Py *et al*., 1987). Scales normally occur on leaf undersides but may be found on the upper leaf surfaces if plants are shaded. Yellow spots may develop on leaves when scale densities are low. Scales have their greatest impact on the ratoon crops, where suckers and fruit may be damaged if

shaded. Heavy pineapple scale infestations may weaken and stunt plants, producing a grey appearance and foliage dieback. Scale infestations may be found on the bottom eyes of mature fruit and all over lodged ratoon fruit (Waite, 1993). Cracks between fruitlets may develop when fruit are highly infested (Linford *et al*., 1949; Py *et al*., 1987). Volunteer plants that emerge next to ratoon plants may exhibit high scale densities.

In addition to chemical controls, this pest may be biologically controlled by natural enemies (Waite, 1993). Tiny wasps, including *Aphytis chrysomphali* (Mercet), *Aphytis diaspidis* (Howard) and *Aspidiotiphagus citrinus* (Craw) (Hymenoptera: Aphelinidae), parasitize the scales, resulting in scale death (Zimmerman, 1948). Ladybirds, such as *Rhyzobius lophanthae* Blasid. and *Telsimis nitida* Chapin (Coleoptera: Coccinellidae), also prey upon the scales (Carter, 1967; Waite, 1993). Routine monitoring programmes should be implemented to detect pineapple scale throughout the crop cycle (Waite, 1993).

Other scales have been reported infesting pineapple but these are not normally a problem. The brown (or red) pineapple scale, *Melanaspis bromeliae* (Leonardi), is similar in appearance to *D. bromeliea* (pineapple scale), but it is a chocolate-brown colour with an elevated centre (Carter, 1967). The Boisduval scale, *Diaspis boisduvalii* (Signoret), may be found on numerous plant hosts and has been reported in Latin America, West Africa, Hawaii, Sri Lanka and Taiwan (Py *et al*., 1987). Nigra scale (also known as black-coffee scale), *Parasaissetia nigra* (Nietner), may be found on pineapple (Zimmerman, 1948).

Rutherglen bug and grey cluster bug

The Rutherglen bug, *Nysius vinitor* Bergroth, and the grey cluster bug, *Nysius clevelandensis* Evans (Hemiptera: Lygaeidae), are found in most production areas where pineapple is grown, except Hawaii (Waite, 1993). These insects are similar in appearance. They are 4 mm in length in the adult stage, have narrow bodies and two pairs of transparent, shiny wings and are attracted to lights. The adults may lay as many as 400 eggs on the flowers and seeds of their crop hosts and weeds. Eggs hatch about 7 days after deposition. The immature nymphs are wingless and pass through five developmental stages (instars) before becoming adults, in about 4 weeks. If their food source diminishes prior to reaching the adult stage, the nymphs may crawl about 99 metres in search of acceptable plant hosts. Pineapple is not one of their preferred host plants (Waite, 1993).

These insects typically increase in numbers in the springtime, and that is when they are a problem (Waite, 1993). Populations initially develop in weeds during the winter and move into pineapple as weeds die off. Rutherglen bugs may be visible on roadside weeds before moving into pineapple plantings. The bugs suck sap from pineapple leaves, which exhibit severe yellow spotting (almost blistering) of the leaf surface. Under severe feeding pressure, leaves may wilt and die. Damaged fruit may exhibit gummosis.

Weather can have an impact on bug populations, and chemical controls are not normally needed (Waite, 1993). High densities are generated during periods of wet winters and hot, dry springs. However, heavy rains can decimate populations.

Good control of host weeds reduces the chances for problems from these bugs (Waite, 1993). Crops should be routinely monitored for these species, especially if large numbers of adult bugs are attracted to house lights at night in the area. Severe infestations may be suppressed with conventional insecticides (Waite, 1993).

Root rots

Root rots may be caused by *Phytophthora cinnamomi* and various *Pythium* species, with *Pythium arrhenomanes* Drechs. as the most common (Klemmer and Nakano, 1964). Initial symptoms are a reduction or elimination of growth, with subsequent reddening of the leaves, the leaf margins turning yellow and eventually becoming necrotic. With *P. cinnamomi*, which causes heart and root rot, the root-rot phase results in reduced plant

growth and yields and, in cooler environments, can result in a total loss of the ratoon crop. Root-rot symptom development is relatively slow in comparison with heart-rot symptoms. Disease from both pathogens is most severe when soils are cold and poorly drained. If environmental and soil conditions become dry following the infection period, affected plants may appear reddish, as if under severe drought stress. Plant anchorage in the soil is very poor following loss of roots.

Early root-health management

With the discovery of the soil fumigant 1,3-dichloropropene, 1,2-dichloro-propane, (DD mixture) pineapple nematodes were easily and economically controlled during the early stages of pineapple plant growth (Carter, 1943; Keetch, 1979; Johnson and Feldmesser, 1987; Caswell and Apt, 1989). Today, early nematode control is accomplished by clean fallow, preplant soil fumigation with dichloropropene at 224–336 l ha^{-1} (Fig. 9.17) and postplant application of an approved nematocide (e.g. fenamiphos and oxamyl) by broadcast sprays or drip irrigation (Fig. 9.18; Rohrbach and Apt, 1986; Caswell *et al*., 1990). Effective soil fumigation requires good plant-residue management and soil preparation (Fig. 9.19). The discovery and use of the inexpensive DD control may have affected the development of other methods of nematode management for pineapple, such as cover crops, crop rotation and host-plant resistance. Crop rotations and resistance have been examined but not researched in depth or used (Caswell and Apt, 1989; Caswell *et al*., 1990). The root-knot, reniform and root-lesion nematodes have relatively large host ranges. Thus, crop rotations are of value only if crop susceptibilities are known.

Root rots are controlled by improving soil water management, including raised beds, deep cultivation and improving surface-water drainage. The fungicide fosetyl aluminium has shown good control of *P. cinnamomi* root rot (Rohrbach and Schenck, 1985). The soil fumigant mixture of DD (Telone) was shown to reduce root rot caused by *P. arrhenomanes* (Anderson, 1966).

Mealybug wilt is readily managed by controlling ants, which tend and protect mealybugs, with an approved insecticide bait (e.g. hydramethylnon) (Rohrbach *et al*.,

Fig. 9.17. Nematode control using preplant soil fumigation under plastic mulch.

Fig. 9.18. Postplant drip irrigation and application of postplant nematocides.

1988). The use of bait stations in an IPM approach increases the efficiency of insecticide use and reduces environmental impacts (G. Taniguchi, personal communication).

Fungal and bacterial heart rots

Fungal heart rot

Fungal heart rots ('top rot' in Australia), as well as root rot of pineapple, are diseases associated with wet environmental conditions. *P. cinnamomi* Rands requires cool conditions and heavy, wet, high-pH soils. Heart-rot mortality can range from 0 to 100%, depending on the soil type, pH and rainfall. The economic impact of heart rot results from a reduction in plant densities due to plant mortality. However, adjacent plant mortality is partially compensated for by increased exposure of the remaining plants and subsequent increased fruit size (K.G. Rohrbach, unpublished results).

Heart rot can be caused by *Phytophthora nicotianae* B. de Haan var. *parasitica* Dast. Waterh., frequently called *Phytophthora parasitica* Dast. in the pineapple literature, *P. cinnamomi* Rands and *Phytophthora palmivora* (Butler) Butler. Heart-rot symptoms are the same, regardless of the *Phytophthora* species causing them. The most widely distributed species are *P. cinnamomi* and *P. nicotianae* B. de Haan var. *parasitica* (Rohrbach, 1983; Rohrback and Apt, 1986). *P. palmivora* probably has a much more limited distribution (Boher, 1974; Rohrbach, 1983). Descriptions of the three pineapple pathogens can be found in Waterhouse (1963) and there is a useful key to identification in Newhook and Stamps (1990).

As pathogens of pineapple, *P. nicotianae* var. *parasitica*, *P. palmivora and P. cinnamomi* are not normally found together. *P. nicotianae* var. *parasitica* and *P. palmivora* are found at lower elevations in Hawaii and in the lowland tropics, where optimum temperatures for disease development are in the range of 25–36°C. In contrast, heart rot from *P. cinnamomi* is found under cooler conditions, such as the higher elevations of Hawaii and the cooler pineapple-production areas, such as Australia, where optimum soil temperatures for disease development are 19–25°C.

An initial heart-rot symptom is the failure of the young leaves to elongate. Later symptoms are yellowing to bronzing of the young leaves, which may then lean to one side of the plant (Fig. 9.20). A slight pull on the young symptomatic leaves will remove them from the plant, confirming the presence of the disease. *Phytophthora* infections are limited to the stem and basal white portion of the leaves.

The primary inoculum of the three *Phytophthora* species is chlamydospores, either alone or in infested plant debris in the soil, where they can survive for years. Chlamydospores of *P. cinnamomi* have been quantified in pineapple soils by sieving (McCain *et al*., 1967). Inoculum levels of five to ten chlamydospores per gram of soil have resulted in approximately 100% infections in non-pineapple hosts (Mitchell and Kannarischer-Mitchell, 1983). Sporangia produced from chlamydospores can be dissemi-

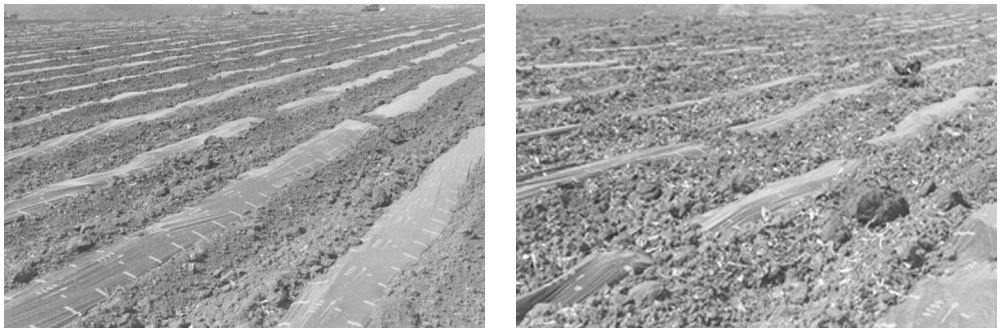

Fig. 9.19. Good (left) vs. poor (right) soil preparation prior to fumigation. Poor soil tilth with large clods results in significant loss of soil fumigant and ineffective nematode control.

Fig. 9.20. *Phytophthora* heart rot caused by *Phytophthora nicotianae* var. *parasitica*.

nated by splashing soil or by aerial wind dispersal. Infection by zoospores of *P. nicotianae* var. *parasitica* is most common through the leaf axils of the crown during the first 3–4 months following planting (H. Klemmer, unpublished results). Infection by *P. cinnamomi* is mostly through the roots, progressing up the root to the stem apex, causing the heart-rot symptom. With *P. cinnamomi*, germinating chlamydospores or zoospores from sporangia primarily infect root tips. Infection may also occur through the leaf axils. Little evidence exists for secondary spread from infected crowns (Chellemi *et al*., 1988).

Very little is known about the effects of soil moisture on infection. Infection by *P. nicotianae* var. *parasitica* is probably less dependent on high moisture than that by *P. cinnamomi* (Hine *et al*., 1964). In citrus, the duration of saturated soil conditions is more important than the frequency. High soil moisture (poor drainage) increases infection by *P. cinnamomi* but also reduces root growth. H. Klemmer (unpublished results) claimed that infections in the field can take place through leaf axils from soil splashed there and moisture from dews. Soil moistures below 15% reduce germinability of *P. cinnamomi* chlamydospores (McCain *et al*., 1967).

Bacterial heart rot

Bacterial heart rot of pineapple is caused by the facultative anaerobe *E. chrysanthemi* Burkh. *et al*. The disease was first reported in Malaysia but has more recently been reported in Costa Rica (Chinchilla *et al*., 1979), Brazil (Melo *et al*., 1974), and the Philippines (K.G. Rohrbach, personal observation). The disease is of major importance in Malaysia but not as important as fruit collapse, caused by the same organism. Recently the disease has become a major problem in the Philippines (K.G. Rohrbach, personal observation).

In Malaysia, bacterial heart-rot incidence varies from 0 to 10% in the 'Singapore Spanish' cultivar and is as high as 30% in the 'Gandul' cultivar (Lim, 1985). Incidence in the 'Smooth Cayenne' cultivar is less because it is more resistant than the 'Spanish' types. Because the plant usually survives infection, the economic loss is attributed to 'out-of-cycle' fruiting on the lateral shoot, which arises from the remaining stem tissue. In mechanized production systems, this 'out-of-cycle' fruit is usually lost.

E. chrysanthemi is a pathogen of a wide range of plants in the tropics and subtropics. This may be due to its ability to grow at higher temperatures than the other soft-rot bacteria. Virulence is related to the ability of *E. chrysanthemi* strains to produce large quantities of endopolygalacturonic trans-eliminase (Perombelon and Kelman, 1980).

Bacterial heart rot is characterized first by a water-soaked lesion on the white basal portion of the leaves of the central whorl. The infection may spread to include the entire basal portion of all leaves of the central whorl. Spread may occur into the green mid-portion of the leaves, resulting in an 'olive-green' leaf colour and a bloated appearance (Plate 28). If the infection of the green portion of the leaf is arrested, a dark infection border forms (Lim, 1985). Symptoms of fungal heart rots can be distinguished from those of bacterial heart rot by the absence of extension of the infection into the mature green areas of the leaf (see Plate 28).

The main source of inoculum is thought to be infested juice from collapsed fruit. Infested seed material is probably not a major source of spread because bacteria do not survive long on leaf surfaces (Lim, 1985). According to Lim (1985), infection takes place through the stomata and the bacteria can be transmitted to the infection site by insects, most commonly ants (the big-headed ant and the Argentine ant), and by wind and wind-blown rain. Souring beetles (*H. ocularis* and *Carpophilus foveicollis*) have also been shown to be vectors, but are of minor importance (Lim, 1985). In the Philippines, the pineapple tarsonemid mite, *S. ananas*, has been associated with bacterial heart rot. Feeding by the mite probably produces wounds, because mechanical wounding is observed to increase disease (K.G. Rohrbach, personal observation). In Australia, urease in dirty water breaks urea down to NH_4OH, which causes burn and provides a point of entry for the bacteria (D. Bartholomew, personal communication). Plants that are 4–8 months old appear to be the most susceptible to infection. The plant crop is also more susceptible than the ratoon (Lim, 1985). Susceptibility appears to be related to the rate of plant growth, because low leaf water status slows the rate of infection (Perombelon and Kelman, 1980). When environmental conditions are optimum for disease development, the entire disease cycle may occur in 1–2 weeks (K.G. Rohrbach, personal observation).

Management of heart rots

Prior to the development of modern fungicides, any method of improving soil drainage was used to reduce disease. Raised beds, ranging from a few centimetres to 25 cm or more, have been used. Improvements in surface drainage, whereby depressions are drained by cutting of ditches or filling to eliminate standing water, have reduced disease levels (Pegg, 1969). Cultural practices such as pineapple-trash mulch have generally, but not always, increased disease incidence.

The addition of elemental sulphur to soil decreased heart rot when the soil bacteria *Thiobacillus* was present to oxidize the sulphur (Pegg, 1977). The addition of sulphur drastically lowers soil pH (below 3.8), which results in reduced sporangial formation and

an explosion of *Tricoderma* sp. Various copper fungicides have been tried for heart-rot control, but, due to the sensitivity of pineapple to elemental copper, have not been used.

Early organic fungicides used for heart-rot control were fenaminosulf (Dexon®), captan and the dithiocarbamates (Pegg, 1969). More recently captafol (Difolatan®), metalaxyl (Ridomil®) and fosetyl aluminium (Allette®) have been used (Rohrbach and Schenck, 1985). Currently, fosetyl aluminium is used very effectively as a preplant dip at rates of 2.24 kg active ingredient (a.i.) 935 l^{-1} (see Fig. 9.13). Initial control from the preplant dip can be extended by foliar applications with rates of 6.72 kg ha^{-1} in 2805 l of water at intervals of 3–6 months. Because fosetyl aluminium acts systemically in the pineapple plant, excellent control of *P. cinnamomi* root rot can be obtained (Rohrbach and Schenk, 1985; Rohrbach and Apt, 1986).

The active ingredient of fosetyl aluminium is phosphorous acid, which will result in comparable control to the parent material (Rohrbach and Schenck, 1985). In Australia, a formulation of phosphorous acid (Phos-forpine® or Fosjet 200®) is used. Because many growers do not have dipping equipment, preharvest sprays are used to systemically protect crowns for planting following fruit harvest (D. Bartholomew, personal communication).

The fungicide metalaxyl has also been shown to be very effective for heart-rot control as a preplant 'seed-piece' dip (Rohrbach and Schenck, 1985). Postplant foliar applications of metalaxyl, although effective, have not been recommended or registered because of the possibility of development of resistant strains of *Phytophthora*.

Several cultivars resistant to *Phytophthora* were developed at the Pineapple Research Institute of Hawaii (PRI). The cultivar designated '53–323' with resistance to *P. cinnamomi* was a cross between 'Smooth Cayenne' and F-236. F-236 was an introduced native variety from Columbia called 'Pina de Castilla', which was collected for PRI by Harold St John. The cultivar '53–323' is highly resistant to *P. cinnamomi* but highly susceptible to *P. parasitica*. A second cultivar, designated '59–656', is resistant to both *P. cinnamomi* and *P. parasitica*. Both cultivars have fruit characteristics and quality similar to those of 'Smooth Cayenne' and yields at least equal to 'Smooth Cayenne' when that variety is grown without occurrence of heart rot or root rot (Pineapple Research Institute of Hawaii, unpublished results).

Sanitation is an important factor in preventing initial low incidences of bacterial heart rot from causing an epidemic. Infected plants should be destroyed or removed from the field, as they may provide a source for secondary inoculum. Crowns or slips from plants with symptoms of fruit collapse or from an area having high a incidence of fruit collapse should not be used as seed material. Mechanical leaf damage, such as occurs when entering a field for crop logging, should be minimized during periods of susceptibility and when low levels of disease are present (K.G. Rohrbach, personal observation).

Partial control of bacterial heart rot has been obtained with miticides (e.g. endosulphan) and insecticides in the Philippines (K.G. Rohrbach, personal observation). Bordeaux mixture has resulted in variable control (Lim, 1985).

In subtropical climates, where the disease is a problem, the resistant 'Smooth Cayenne' cultivar might be used rather than the much more susceptible 'Spanish' types (Lim, 1971). However, in the lowland tropics, 'Smooth Cayenne' is difficult to force and may have poor fruit quality, thus limiting its use.

Yellow spot (tomato spotted-wilt virus)

Yellow spot of pineapple occurs in all production areas of the world, with the exception of peninsular Malaysia (Lim, 1985). Infection by the tomato spotted-wilt virus always kills the pineapple plant. Therefore, vegetative propagation does not transmit the virus to subsequent plantings (Rohrbach and Apt, 1986).

Pineapple yellow-spot disease, caused by the tomato spotted-wilt virus, was first observed in Hawaii as a distinct disease in 1926 (Illingworth, 1931). During the next 4 years, the disease spread and became a serious problem, with considerable rotting of fruits in the field.

The initial symptom is a slightly raised

yellowish spot, with a darkened centre, on the upper surface of the leaf. Shortly after formation of the initial spot, a characteristic chain of secondary spots develop and progress into a basal leaf and stem rot. Frequently, particularly on young plants, the rotting and cessation of growth on one side of the stem cause the plant to bend severely, eventually killing the entire plant (Plate 29). The disease can occur on the developing crown, with the rot progressing into the fruit and frequently causing distortion of the fruit (Illingworth, 1931).

Infection occurs most frequently on pineapple plants during early growth. On occasion, crowns on developing fruit may also become infected (Linford, 1943). The transmission of the yellow-spot virus by the onion thrips, *Thrips tabaci* (Lindeman), was shown in 1932 by Linford. Pineapple is not a preferred host of thrips, but the thrips still move into pineapple fields from adjacent weed hosts and probe the plants, leaving the virus in the tissue (Linford, 1932). Later, the yellow-spot virus was shown to be identical to the tomato spotted-wilt virus (Sakimura, 1940).

Thrips

As many as 39 species of thrips have been reported worldwide in and around pineapple fields (Sakimura, 1937; Carter, 1939; Petty, 1978d). Wind currents may carry many individuals of these species from their host plants (e.g. domestic crops, ornamentals, weeds) into adjacent pineapple plantings (Carter, 1939). However, most of the thrips do not normally feed or reproduce on pineapple. Sakimura (1966) only reports six thrips species commonly living within Hawaiian pineapple plantings. These include the onion (or potato) thrips, *T. tabaci* (plant feeder), leaf thrips, *Frankliniella sulphurea* Schmutz (flower feeder), *Thrips hawaiiensis* (Morgan) (flower feeder), *Aleurodothrips fasciapennis* (Franklin) (predator on scales), *Haplothrips melaleucus* (Bagnall) (predator on scales) and *Haplothrips gowdeyi* (Franklin) (flower feeder). Species reported as vectors of tomato spotted-wilt virus, which causes yellow spot on pineapple, are the onion thrips and the common blossom thrips (also known as kromnek thrips, cotton-bud thrips, yellow-blossom thrips), *Frankliniella schultzei* (Trybom) (Sakimura, 1963; Petty, 1978d). Py *et al.* (1987) state that one of the vectors of yellow spot, the tobacco thrips, *Frankliniella fusca* (Hinds), is established in Hawaii (based on a reference by Sakimura, 1966) but this is incorrect (D. Tsuda, personal communication). Additionally, the western flower thrips, *Frankliniella occidentalis* (Pergande), is established in Hawaii (as indicated by Py *et al.*, 1987), but has not been reported as a vector of yellow spot on pineapple.

Pineapple yellow spot can be controlled by maintaining a weed-free production system to eliminate the weeds that serve as virus reservoirs. Adjusting the timing of operations of adjacent crops as well as pineapple to minimize the movement of thrips vectors into the pineapple fields aids in the reduction of inoculum (Rohrbach and Apt, 1986).

Three Months to Forcing

Weeds

Depending on weed species present and rainfall during the first 3 months of growth, a second broadcast spray may be applied (e.g. diuron, ametryne). Most weed problems during this period are escapes from the initial application at planting and the 3-month application. Escapes are usually controlled by spot applications (Glennie, 1991).

Nematodes

The root-knot nematode may cause significant root damage during the first few months of root growth. Initial infections occur at the root tip in the meristematic region and result in termination of growth of the primary root. Unless plants are subjected to water and/or severe nutrient stress, above-ground symptoms of early nematode infection will not be evident (Caswell *et al.*, 1990). Severely infected plants can be pulled from the soil and terminal galls will be evident on primary roots.

Root infection by the reniform nematode does not cause termination of primary root

growth, as does root knot, but affects secondary root growth. Thus, symptoms of reniform infection will not become evident until 6 or more months of growth and again only under water and/or nutrient stress (Caswell *et al.*, 1990).

In Australia, yield losses occurred where root-knot nematodes were detected from 9 to 15 months following planting, suggesting that sampling may be important in determining the need for postplant nematocide applications (Stirling and Nikulin, 1993). While soil sampling during plant growth (to estimate nematode populations) should be important for nematode management, in practice postplant nematode control is frequently applied as 'insurance', based on qualitative data, along with historical yield and nematode population information. The non-volatile nematiocides, such as oxamyl and fenamiphos, may be applied postplant as foliar sprays or through drip irrigation systems (Caswell and Apt, 1989).

Ants and mealybugs

Where adequate mealybug biological controls exist (see section above on mealybugs), controlling ants results in control of mealybugs and therefore mealybug wilt. Mealybug wilt is readily managed by controlling ants with an approved insecticide bait (e.g. hydramethylnon) (Rohrbach *et al.*, 1988). Baits are primarily applied to field borders and only inside fields when ants have become established. The use of bait stations in an IPM approach to control increases the efficiency of insecticide use and reduces the environmental effects (G. Taniguchi, personal communication).

Forcing to Flowering

Because of the anatomy and morphology of the pineapple inflorescence and fruit, a wide range of microorganisms can be found on the surface of the developing inflorescence and, following anthesis, inside the developing pineapple fruitlet (see Plate 30). Initially, the developing inflorescence is essentially sterile. As the inflorescence enlarges and extends out of the vegetative growing point or 'plant heart', the entire surface becomes contaminated with a multitude of microorganisms and fauna (Fig. 9.21) (K.G. Rohrbach, unpublished results).

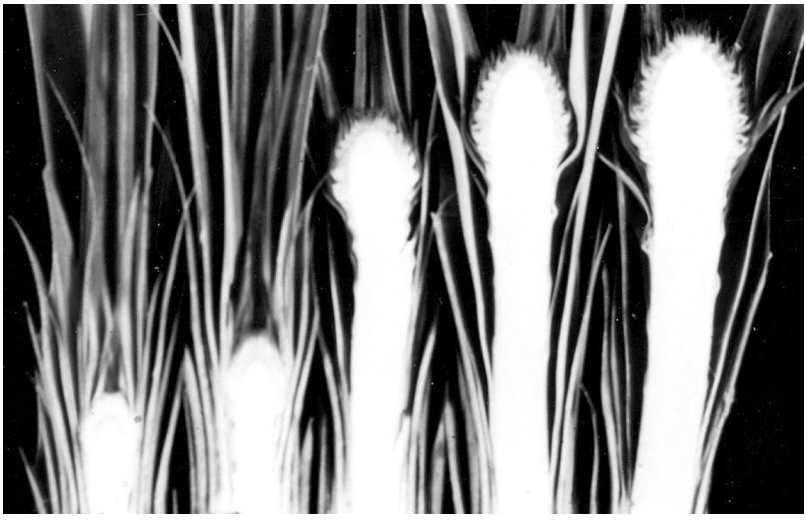

Fig. 9.21. Commercial stages of pineapple inflorescence development denoted as 1.3 cm open heart, 2.5 cm open heart, early cone, mid-cone and late cone (left to right). Each stage is approximately 1 week's growth from the previous one.

Fruitlet core rot, leathery pocket and interfruitlet corking

Three strains of *Penicillium funiculosum* have been reported associated with pineapple fruitlet core rot (FCR), leathery pocket (LP) and interfruitlet corking (IFC) and have been found on withered flowers, the plant heart, pineapple trash and insects and mites found in pineapple fields (Lim and Rohrbach, 1980).

The disease cycle of *P. funiculosum* starts with the presence and build-up of the pineapple tarsonemid mite, *S. ananas*, in the plant heart during growth. Mites feed on the developing trichomes on the basal portion of the leaf in the plant heart and on bracts and sepals of the developing flowers on the inflorescence. Mite populations peak at 6–7 weeks following forcing when the inflorescence is emerging (Plate 30; Fig. 9.21). The virulent strain (P1) of *P. funiculosum* must be present by 1 week following forcing in order to colonize the mite-injured trichomes and have sufficient inoculum potential to grow into the unopened flower. Infection occurs through the developing flower at 1–2 weeks prior to normal anthesis (Fig. 9.22; Rohrbach and Apt, 1986). The optimum temperature for infection is 16–21°C during the 6 weeks following forcing. Moisture does not appear to be critical during this period (Petty, 1978c). Following infection, the fungus develops in the internal flower parts.

F. subglutinans is a soil fungus, but, like *P. funiculosum*, may also colonize the heart of the growing pineapple plant. *F. subglutinans* may survive for up to 12 months in pineapple tissues. In contrast to *P. funiculosum* growing into the unopened flower, infection by *F. subglutinans* apparently takes place only through the open flower, although colonization in the heart of the plant and on the inflorescence must occur prior to open flower (Ventura *et al*., 1981).

Cultivars vary in their symptom responses to infection by *Penicillium* and *Fusarium*. In Hawaii, the 'Smooth Cayenne' cultivar generally has relatively low levels of FCR but high levels of IFC and LP from *Penicillium* infection. In contrast, the hybrid '53–116' ('NCGR No. 159') has high LP and IFC but low FCR. The hybrid cultivar '58–1184' ('NCGR No. 160') has very little IFC and high FCR, especially when infections are caused by *Fusarium*.

Mites

The pineapple tarsonemid mite, *S. ananas*, only infests pineapple plants (see Fig. 9.11; Jeppson *et al*., 1975). It occurs universally on

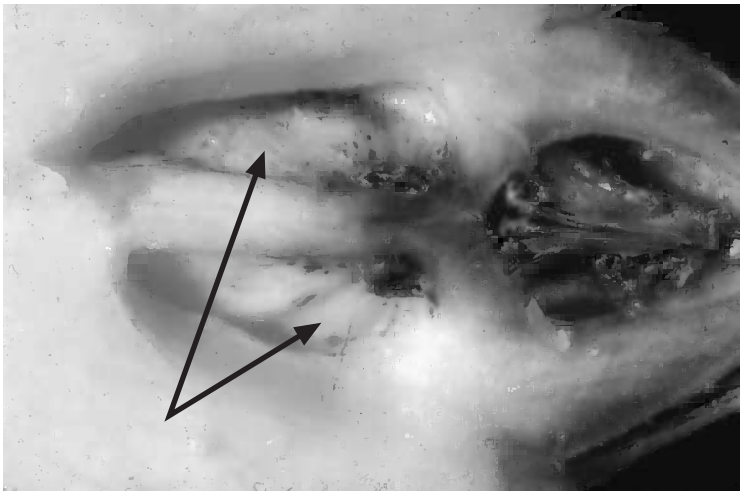

Fig. 9.22. Cross-section of *Penicillium funiculosum*-infected flower showing rotting of internal flower parts and beginning of leathery pocket in locules (arrows).

the growing plant, developing inflorescence, fruit and crown. The pineapple tarsonemid mite is most abundant from just prior to flower induction (forcing) through the 12.7 mm and 25.4 mm open-heart stages of inflorescence development (see Fig. 9.21) and flowering. It is grey in colour and the body of the adult mite is oblong, 0.125 $\times$0.25 mm and flat. The life cycle is 7–14 days, depending on temperature. Pineapple tarsonemid mites feed on developing trichomes on the white basal-leaf tissue and flower bracts and sepals, causing light brown necrotic areas. Mites may also enter the infected flower and feed on internal flower parts. The young developing inflorescence cone seems to be the preferred feeding site (Petty, 1975, 1978c; Rohrbach and Schmitt, 1994).

Very high populations of pineapple red mite, *D. floridanus*, are always associated with epidemics of *Fusarium* fruitlet core rot in Hawaii (see Fig. 9.10; K.G. Rohrbach, personal observation). The association between the pineapple red mite and *F. subglutinans* FCR is not understood. No cause-and-effect association has been demonstrated.

Control of the pineapple tarsonemid mite is important to the control of *P. funiculosum*-induced FCR, LP and IFC. Endosulphan (Thiodan®) applications at 3 weeks prior to and 1–5 weeks following forcing have resulted in the best control of *P. funiculosum*-induced diseases (Le Grice and Proudman, 1968; Le Grice and Marr, 1970; Rohrbach *et al*., 1981). Petty (1990) also reported reductions in the incidence of disease symptoms (leathery pocket) caused by *P. funiculosum* following applications of the miticide endosulphan, which suppressed the pineapple tarsonemid mite in South African pineapple plantings. Jeppson *et al.* (1975) observed that species in the genus *Steneotarsonemus* are not typically controlled by sulphur but show great susceptibility to organophosphate acaricides or the halogenated thioether group.

Flowering to Harvest

The pineapple flower is a primary portal for the entrance of several fruit-disease pathogens (Fig. 9.23). At anthesis, openings occur via the stylar canals and nectary ducts into the locules and nectary glands, respectively. These openings become the primary sites for infection by the bacterial and fungal fruit-disease pathogens. The susceptibility of these infection sites depends on environmental conditions, as they affect the predisposition of the flower and the occurrence of the pathogen on the flower. Occurrence of the pathogen on the flower may be dependent on an insect vector or development of the pathogens on the inflorescence prior to anthesis.

The multiple requirements for flower infection are: (i) a means of getting the pathogen to the susceptible flower; (ii) a susceptible flower at the right time; and (iii) optimal environmental conditions for disease development for each factor. These multiple requirements have resulted in complex aetiologies and very sporadic occurrence of the fruit diseases.

Pink-disease, fruit-collapse and marbling-disease bacteria

Pink disease

Pink disease is of little importance in fresh fruit, but can be a very serious sporadic problem in processed fruit because of the lack of

Fig. 9.23. Pineapple inflorescence at mid- to late flower.

detection prior to canning. It was first reported in Hawaii by Lyon (1915) and is now known in Australia, the Philippines, South Africa and Taiwan (Rohrbach, 1983). Cultivars vary in their susceptibility (Rohrbach and Pfeiffer, 1975). At least three genera of bacteria have been reported to cause pink disease: *Erwinia*, *Gluconobacter* and *Acetobacter* (Rohrbach, 1976a; Kontaxis and Hayward, 1978). The *Erwinia herbicola* species has recently been redescribed as *Pantoea citrea*, based on an isolate from the Philippines (Cha *et al*., 1997). Species of the remaining genera are the acetic acid bacteria *Gluconobacter oxydans* and *Acetobacter aceti* (Plate 31; Cho *et al*., 1980).

Pink-disease bacteria are vectored to the pineapple flowers by insects and mites, probably attracted to the nectar. Honey-bees may play a role as important vectors of *Gluconobacter* and a lesser role for *Acetobacter* (Gossele and Swings, 1986). The nectar is thought to provide a nutrient source for the survival of the bacteria until they become latent in the nectary gland or stylar canal or locule. Gossele and Swings (1986) suggest that the bacteria may actually overwinter in honey-bee hives. Once the bacteria are inside the flower, they remain latent until the fruit matures, sugar concentrations increase and translucence occurs.

Fruit collapse

Bacterial fruit collapse, caused by *E. chrysanthemi* Burkh. *et al*., is only economically important in peninsular Malaysia, although the bacteria have been reported elsewhere on pineapple (Melo *et al*., 1974; Chinchilla *et al*., 1979; Rohrbach, 1983). The disease is thought to be indigenous to Malaysia (Lim and Lowings, 1979b). The economic importance of fruit collapse in Malaysia is probably due to the use of the much more susceptible 'Singapore Spanish' cultivar (Lim, 1985).

Symptoms of fruit collapse usually appear on maturing fruit 2–3 weeks prior to normal ripening (Plate 32). Infected fruit are characterized by exudation of juice and release of gas, as evidenced by bubbles. Fruit shell colour becomes olive-green. Dissection of completely infected fruit shows only cavities within the skeletal fibres of the fruit (Lim, 1985).

Bacterial fruit collapse is caused by *E. chrysanthemi* Burkh. *et al*., and the initial inoculum comes from other infected fruit. Insects such as ants, beetles and flies, are vectors of the bacteria, transporting them to flowers from other collapsed fruit or from plants with bacterial heart rot. Ants, as well as other insects, are thought to be attracted to the nectar available there. Open flowers are the infection site where the bacteria enter the developing fruit. The bacteria remain latent in the ovary until 2–3 weeks before normal ripening when sugar levels begin to increase rapidly and polyphenoloxidase levels decline (Lim and Lowings, 1978).

Marbling disease

Marbling disease is a sporadically occurring pineapple disease of the hot, humid, lowland tropics. Symptoms include a brown granular appearance (Plate 33). Marbling disease is caused by the acetic acid bacteria *Acetobacter peroxydans* Visser 't Hooft and *E. herbicola* var. *ananas* (Serrano) Dye. As in pink disease, infection by marbling bacteria occurs through the open flower (Rohrbach and Pfeiffer, 1974). Infection has also been reported within 7 weeks of harvest through growth cracks in the fruit (Yow and Wu, 1972), although this was not confirmed in Hawaii (Rohrbach, 1989). Speculation exists that the bacteria are vectored to the flowers by insects, as in pink disease (Serrano, 1928). The fact that application of surfactants prior to and during flowering significantly increases disease in Hawaii without inoculation indicates that the bacteria are ubiquitously present on the plant and that the limiting factor is whether they get into the flower. Once in the flower, as with pink disease, they apparently remain latent until approximately 1 month before fruit maturity. Symptoms develop during the last month of fruit maturation (Rohrbach, 1989).

Management of bacterial diseases through flowering to harvest

Pink disease has been controlled with insecticides, which are thought to control insect

vectors. Where pink disease occurs sporadically, insecticide applications have not been economic. In the Philippines, where pink-disease epidemics are seasonally predictable, pink disease has been controlled with applications of disulphoton. Disulphoton at 0.83 kg a.i. ha^{-1} per application starting at the red-bud stage and with three additional applications at 5-day intervals (throughout flowering), has resulted in the highest level of control (Kontaxis, 1978).

Applications of ethephon to inhibit flower opening and reduce nectar flow have resulted in partial but significant control of fruit collapse (Lim and Lowings, 1979a) and pink disease (K.G. Rohrbach, unpublished results). Forcing plantings, so that flowering does not coincide with fruiting in adjacent plantings, which may have fruit collapse, can reduce disease development. Applications of Bordeaux mixture have resulted in variable control (Lim, 1985). Any treatment that reduces bacterial heart rot may reduce primary inoculum levels for flowering plants. Sanitation is an important factor in initial low incidences of fruit collapse. Infected plants and fruit should be destroyed or removed from the field, as they may provide a source for secondary inoculum.

Currently, no known controls of marbling exist. When epidemics occur, infected fruit can be detected and excluded prior to going through the cannery by external appearance and a test to measure fruit firmness, such as sticking a knife into the fruit. If incidences are extremely high, all fruit must be discarded. In contrast to pink disease, infected fruit tissues that are not discarded before processing can be discarded before packing in cans.

Lepidopterous stem and fruit pests

Bud moth, pineapple borer

The bud moth (also known as pineapple borer, pineapple caterpillar), *Thecla basilides* (Geyer), is found throughout Central and South America wherever pineapples are grown (Py *et al*., 1987; Sanches, 1999). While *Thecla* is a tropical species, it could cause problems if imported into the southern USA, particularly Florida, because it has been observed to feed on maize, cacao, *Heliconia* and several other bromeliads (Rohrbach, 1983).

The adult stage of the bud moth deposits its eggs on the inflorescence prior to anthesis. The larva infests the fleshy parts of the bracts and feeds inside the developing inflorescence. Buds and open flowers are entered directly, with larvae penetrating developing fruit and digging out holes of varying depths. This results in malformed fruit, which is unmarketable (Py *et al*., 1987). In response to the actions of the larvae, the pineapple fruit forms an amber-coloured gum (gummosis), which exudes and hardens on contact with the air (Fig. 9.24). This resembles the resin exuded by pine trees (sometimes called 'resinous' by Brazilians). When secondary infections are due to *F. moniliforme* var. *subglutinans*, the exudate is more fluid and glassy, characteristic of fusariosis disease. The pathogen can penetrate the

Fig. 9.24. Fruit showing multiple *Thecla basilides* infestations and resulting gummosis.

inflorescence without the bud-moth larva, but the bud moth makes it easier to do so. Adult bud moths may help disperse the pathogen when visiting healthy plants after visiting diseased ones. Following a 13–16-day feeding period, the larvae emerge and pupate in the leaf axils. Control with insecticides is relatively easy if flowering is uniformly induced with forcing agents. Predators exist in Trinidad, including the vespid wasp *Polistes rubiginosus* Lepeletier and a predator of larvae, *Heptamicra* sp. Another predator reported is *Metadontia curvidentata*. No organized biological-control campaign has been undertaken for the bud moth (Py *et al*., 1987).

Fruit-piercing moth

There are numerous species (> 90) of moths in the lepidopteran family Noctuidae in which the adult stage (i.e. moth) pierces many types of fruit with a specially adapted proboscis (Banziger, 1982). The well-known pest called the 'fruit-piercing moth', which attacks pineapple. is *Eudocima* (= *Othreis*) *fullonia* (Clerck) (also known as *Ophideres fullonica* L.). It does not limit its adult feeding to pineapple and may attack numerous fruits (e.g. oranges, guavas, star fruit, mangoes, bananas, coffee, passion-fruit, lychee, etc.) if available (Waterhouse and Norris, 1987). It may be found in many areas where pineapple is grown (Australia, Asia, Hawaii). The larval stages of the moth do not feed on pineapple, and outside the Pacific Basin they attack at least 30 species of creepers belonging to the plant family *Menispermaceae*. Within the Pacific Basin, the larvae are normally found feeding on coral trees in the genus *Erythrina* (*Fabaceae*) (Cochereau, 1977). They may be found on a creeper, *Stephania foresteri,* which is now rare in New Caledonia. The larval stages feed on the foliage of their host plants, where the yellowish green eggs are also laid. An individual female moth may lay as many as 750 eggs, either singly or in batches of up to 100–200 eggs (Waterhouse and Norris, 1987). Several generations are possible during a year.

Injury to fruit is caused by strongly sclerotized appendages (maxillae) at the end of the approximately 25.4 mm proboscis. The tips of the maxillae are equipped with a series of teeth and spines, which enable the adult moth to rasp a hole through the tough skin of the pineapple fruit. The act of piercing the fruit requires little time, from several seconds to a few minutes (Cochereau, 1977).

Controlling *E. fullonia* is difficult, with pesticides normally being ineffective, since the larval stages of the pest are not within the pineapple crop. Pesticides applied to the ripe fruit can also cause human-health concerns, due to the presence of toxic residues (Waterhouse and Norris, 1987). Several approaches have been tried for the control of fruit-piercing moth, but none are especially effective or, if so, they are impractical or expensive to implement. These include use of poison baits for control of the adult stage; confusing searching adults by masking fruit volatiles in orchards with smoke; use of potential repellents; orchard sanitation to reduce quantities of decaying or fallen fruit; early harvest of fruit; hand-capturing and killing of moths; bagging of fruit; using floodlights to disrupt moth flight behaviour; and eradication of host plants (Baptist, 1944; Cochereau, 1972a; Banziger, 1982). Where natural enemies exist and conditions are favourable, biological control has proved effective in New Caledonia (Cochereau, 1972b, 1977). Natural enemies include parasitoids and predators of eggs and larvae, as well as a fungal disease of the eggs (*Fusarium* sp.). Egg parasitoids in the genera *Ooencyrtus* (Hymenoptera: Encyrtidae) and *Trichogramma* (Hymenoptera: Trichogrammatidae), as well as the larval–pupal parasitoid *Winthemia caledoniae* Mesnil (Diptear: Tachinidae), are excellent candidates for introductions into areas where biological control of the pest is poor. Additionally, reduction in the abundance of the larval host plants could help suppress adult numbers within an area (Waterhouse and Norris, 1987).

Giant moth borer

The giant moth borer, *Castniomera* (= *Castnia) licus* (Drury) (Lepidoptera: Castniidae), is found in South America (e.g. Brazil), where it is a minor pest of little economic conse-

quence on pineapple (Collins, 1960). The mature larvae of this species live up to their common name and are about 7.6 cm in length. Larvae may enter the stem of the pineapple plant and burrow vertically into the peduncle, which supports the fruit. This action disrupts fruit production (Collins, 1960). Adult moths have a wing spread of about 12.7 cm.

Pineapple stem borer

An additional lepidopterous pineapple stem borer, *Castnia penelope* (Schaufuss) (= *Castnia icarus* (Cramer)) (Lepidoptera: Castniidae), is reported to occur in several localities in Brazil on pineapple and banana (Sanches, 1981, 1999).

Mites

The blister mite, *P.* (= *V.*) *sakimurae*, may be found on fruit after the flat-eye stage and may eventually become abundant on ripe fruit (Carter, 1967). It prefers to feed within the narrow spaces deep in the interfruitlet grooves, where it attacks hard epidermal tissues. Individuals possess a tiny but powerful piercing stylet and sap is evidently sucked from pierced cells, but no scars are produced (Carter, 1967). These mites can disperse to the pineapple crowns, which are eventually used for seed material (see section above on seed material).

Other stem borers

The larva of the weevil *M. ritchiei* (Marshall), found in the Caribbean, can bore into the pineapple stem of young suckers and emerge from the fruit, completely destroying the plant (Carter, 1967). Another weevil found in South America, *P. crenatus* (Billberg), can cause pineapple stem damage (Sakimura, 1966).

Harvest to Consumer

Most symptoms of pineapple fruit diseases are exhibited following harvest. Many fruit disease symptoms have been described on pineapple (Collins, 1960; Rohrbach and Apt, 1986). The 'Smooth Cayenne' cultivar is relatively resistant to most pineapple fruit diseases. Historically, only black rot and the chilling injury termed 'internal browning' or 'black heart' have been of sufficient economic importance and occurrence to warrant control practices. In a study of disorders of pineapple coming into the New York market between 1972 and 1985, black rot was the most common problem, occurring in 70.3% of the shipments. Severity in affected shipments varied from 11% to 50% rot. Brown rot or fruitlet core rot occurred in only 6.5%. Internal browning occurred in 19.5% of the shipments (Cappellini, 1988). In developing countries, pineapple losses can be as high as 70% (Salunkhe *et al*., 1991).

As with the pineapple plant diseases, fruit diseases are measured by seasonal frequency (occurrence of disease), incidence (presence or absence of disease in a single fruit) and severity (degree of infection or number of affected fruitlets in a single fruit). An index scale (Fig. 9.4) has been developed to quantitatively measure pineapple fruit diseases (Rohrbach and Taniguchi, 1984). The scale is based on the high economic impact of relatively low blemish levels on losses in the cannery, the need to discard severely infected fruit tissue, to increase labour to remove low to moderate blemish levels from fruit cylinders prior to or following slicing and to downgrade the remaining product. Thus, a single blemish in one fruitlet of the fruit cylinder (index value of 1) may downgrade the entire slice from a fancy whole slice to chunks or crush and require additional labour to remove the blemish. Ratings of 2 or 3 essentially eliminate all of the economically more valuable fancy slices from the fruit. Ratings of 4–5 essentially cause the entire fruit cylinder to be discarded. This disease index has been used for all major fruit diseases.

The frequency and incidence of fruit diseases are extremely variable with high levels occurring only sporadically. The sporadic occurrence has severely limited the ability to do research on the aetiology and control of all the fruit diseases. In Hawaii three techniques

have been used to increase the frequency, incidence and severity of the major pineapple fruit diseases for research purposes. First, hybrid cultivars have been identified which are more susceptible to the test pathogens than the relatively resistant 'Smooth Cayenne' cultivar. Secondly, multiple forcing at 2–4-week intervals are used in any single test to increase the probabilities of having susceptible stages of the inflorescence and flowers at times of optimal environmental conditions. Thirdly, inoculations with the test pathogen prior to or at anthesis are made. These techniques have greatly increased the frequency of test conditions and have added considerably to the information about the aetiology of the major pineapple fruit diseases.

Black rot

Black rot, also called *Thielaviopsis* fruit rot, water blister, soft rot or water rot, is caused by the fungus *C. paradoxa* (De Seynes) Sacc. (syn. *T. paradoxa* (De Seyn.) Hohn (telemorph *C. paradoxa* (Dade) C. Moreau). The disease is a universal fresh-fruit problem but normally not a problem with processed fruit, because times from harvest to processing are too short for infection. The severity of the problem is dependent on the degree of bruising or wounding during harvesting and packing, the level of inoculum on the fruit and the storage temperature during transportation and marketing. Black rot does not occur in the field unless fruit is overripe or injured.

Black rot of the pineapple fruit is characterized by a soft watery rot, which usually starts at the point of detachment of the fruit (Fig. 9.25). Diseased tissue turns dark in the later stages of the disease because of the dark-coloured mycelium and chlamydospores.

Infection of the pineapple fruit occurs through wounds resulting from harvesting and postharvest handling. Susceptibility varies, with the 'Red Spanish' types being more resistant than 'Smooth Cayenne'. Under conditions of high humidity, conidia may readily be produced on pineapple residue and be disseminated by wind to the unharvested fruit. Inoculum levels on fruit at harvest vary according to the environmental conditions prior to harvest (Rohrbach and Schmitt, 1994). The high correlation between moisture (rainfall duration) prior to harvest and disease following harvest has resulted in the name 'water rot'. Infection occurs within 8–12 h following wounding. Refrigeration at 9°C during transportation will slow development of the disease, but, when fruit are returned to ambient temperatures, disease development will resume (Rohrbach and Phillips, 1990).

Fig. 9.25. Cross-section of fruit showing black rot caused by *Chalara paradoxa* at the broken peduncle and through a bruise on the side of the fruit.

Fruitlet core rots (black spot)

FCR (Oxenham, 1962; Rohrbach and Apt, 1986) or black spot (Keetch, 1977) (also called fruitlet brown rot and eye rot (Snowdon, 1990)) is a descriptive term for a brown to black colour of the central part of an individual fruitlet (Fig. 9.26). FCR is caused by an infection by a pathogen or, more commonly, a group of pathogens. Botanically the central area of the fruitlet core is the septa (inverted Y) between the three seed cavities or locules (Fig. 9.27).

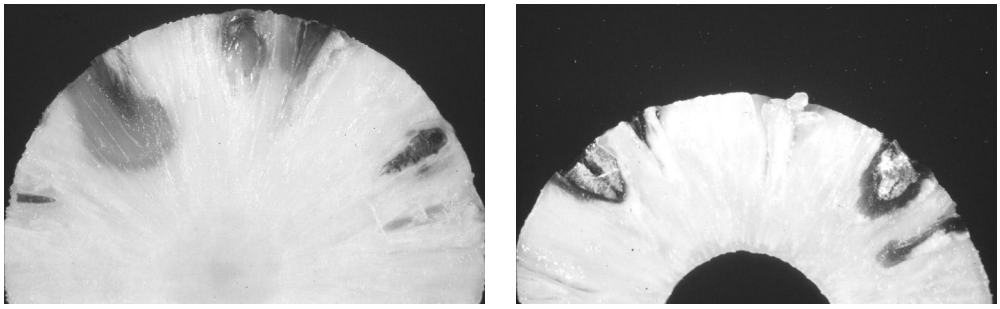

Fig. 9.26. Pineapple fruit slices showing fruitlet core rots caused by *Penicillium funiculosum* (left) and *Fusarium subglutinans* (right).

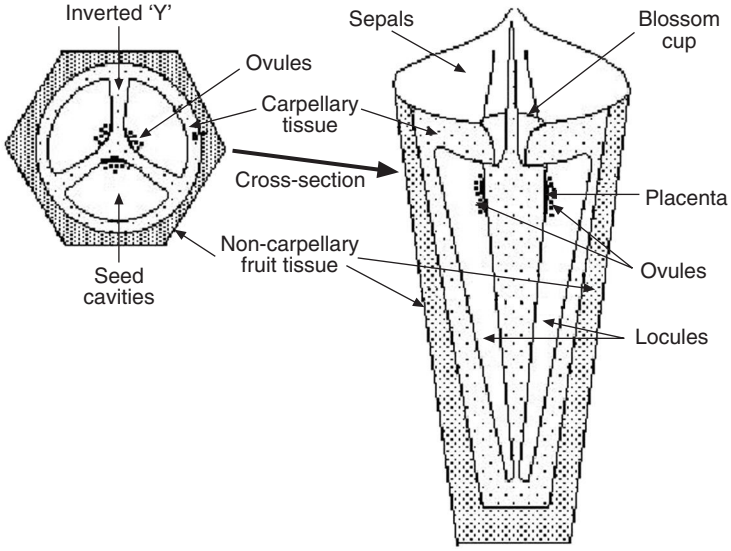

Fig. 9.27. Diagram of a cross-section of a pineapple fruitlet showing the internal parts.

Because individual or mixtures of pathogens may be associated with the FCR symptom, there is considerable confusion in the literature. The *Penicillium* and *Fusarium* fungi (Rohrbach and Apt, 1986), the round yeasts (M. Okimoto, unpublished results) and bacteria (D. Gowing, H. Spiegelberg, I. Yanagihara and J. Darroch, unpublished results) have been associated with the FCR symptom. In addition to the multiple pathogens, two mites have also been reported to be associated with the occurrence of FCR epidemics (Rohrbach and Apt, 1986; K.G. Rohrbach, unpublished results).

Two additional symptoms – IFC (Fig. 9.28) and LP (Fig. 9.29; Hepton and Anderson, 1968; Petty, 1977b) – are clearly associated with FCR caused by *Penicillium* infection (Rohrbach and Apt, 1986). The degree to which these symptoms develop appears to depend on the time of infection, the pathogen or mixture of pathogens present, the cultivar and environmental conditions. The IFC symptom can also be caused by boron deficiency in which case the symptoms are indistinguishable (K.G. Rohrbach, personal observation).

Two distinct levels of FCR occur in commercial production of 'Smooth Cayenne'

Fig. 9.28. Interfruitlet corking caused by *Penicillium funiculosum* infections of the pineapple flower and subsequent reduction of growth of the individual fruitlet (could also be symptoms of boron deficiency).

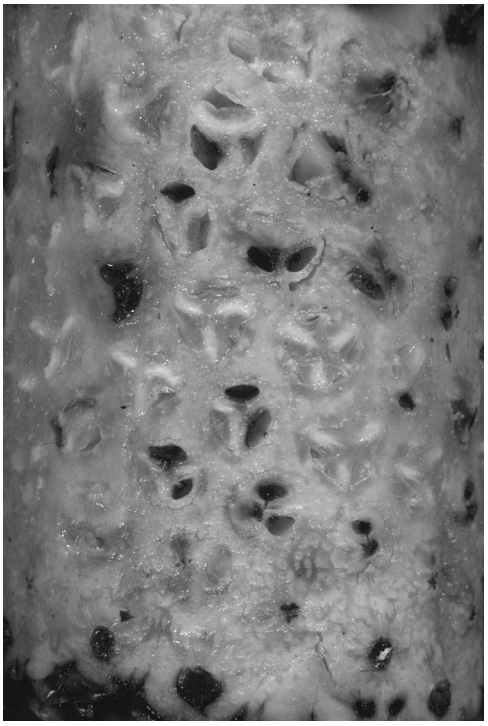

Fig. 9.29. Leathery-pocket symptoms caused by *Penicillium funiculosum* in pineapple fruit cylinder.

(K.G. Rohrbach, personal observation): (i) a very low incidence of one to five fruitlets per 100+ fruits; (ii) a true epidemic, in which every fruit will have at least some FCR and many fruits will have multiple fruitlets infected (25 or more). It is theorized that the very low levels are the result of botanical malformations of individual fruitlets caused by disruptions in the normal phyllotaxis of the fruit (Kerns *et al*., 1936). Malformation of the fruitlet allows infection of the stylar canals and nectary ducts by a range of pathogens. In contrast, true epidemics result from the coincidence of optimum environmental conditions resulting in predisposed flowers, production of inoculum of the pathogen(s) and transport of the inoculum to potential infection sites.

Each major pineapple production area appears to have characteristic pathogens associated with the FCR symptom, probably as a result of the environmental conditions of the area (Rohrbach, 1980). For example, in Hawaii, *Penicillium* and *Fusarium* species are most commonly associated with FCR (Rohrbach and Apt, 1986). In South Africa, *Penicillium* species are most commonly found (Keetch, 1977), while, in Brazil, *Fusarium* species are most commonly associated with the FCR symptom (Bolkan *et al*., 1979).

FCR and associated symptoms are of major economic significance only as epidemics, not at endemic levels. Fortunately, true epidemics are relatively sporadic in the 'Smooth Cayenne' cultivar and in the major commercial pineapple areas of the world. The disease could become more important if some of the more susceptible, low-acid 'Smooth Cayenne' cultivars and hybrid cultivars are grown commercially for fresh-fruit markets.

The FCR symptom is generally characterized by browning of the inverted 'Y' tissues

(septa) between the locules (Fig. 9.27). The degree of discoloration may vary from a very slight brown to dark brown or black. As mentioned previously, the FCR complex involves the fungi *P. funiculosum* and *F. subglutinans*, and the round yeast *Candida guilliermondi*. The pineapple tarsonemid mite, *S. ananas*, and the pineapple red mite, *D. floridanus*, are also associated with the FCR complex. While all of these organisms have been associated with the FCR symptom, little information has been published on the role of the yeasts as pathogens and the role of the pineapple red mite in *Fusarium* FCR. Considerable information is known and published on the *Penicillium*- and *Fusarium*-induced fruit diseases and the role of the pineapple tarsonemid mite (Rohrbach and Pfeiffer, 1976b; Rohrbach and Taniguchi, 1984).

FCR symptoms produced by *Penicillium* species are dark to medium brown in colour, usually with a grey, water-soaked centre (Fig. 9.26). The colouring may extend into the non-carpellary tissue. Blue-green sporulation is frequently observed in the locules on the ovules (see Fig. 9.22). FCR symptoms caused by *Fusarium* species vary in colour from light through medium to dark brown and extend partially to completely down the fruitlet core (Fig. 9.26). FCR caused by *Fusarium* species is usually a 'dry' type of rot, in contrast to the moister and softer *Penicillium* and yeast rots. Inoculations of fruit with *Fusarium* at different stages of development result in different symptoms. Very early infections result in light brown colour, while dark brown colour results from late infections (K.G. Rohrbach, unpublished results). White to pinkish mycelium frequently occurs in the seed cavities (indication of sporulation) (K.G. Rohrbach, personal observation).

FCR symptoms from yeast infections are usually light brown. The same yeasts causing FCR are associated with glassy spoilage (discussed below).

Fusariosis

Fusariosis is caused by the fungus *F. subglutinans* which is the conidial stage of *G. fujikuroi* Edwards. Whether or not *F. subglutinans* in Brazil is the same as the *Fusarium* species causing FCR is not definitive in the literature. Laville (1980) considers *F. subglutinans* a distinctly different species from the *Fusarium* causing FCR. Other authors have attributed FCR to *F. moniliforme* (Oxenham, 1962; Guerout, 1974; Rohrbach, 1983). The disease, first described in Argentina in 1954, was first reported in Brazil in 1964 and within 10 years had spread over the entire country (Laville, 1980; Rohrbach, 1983).

The fruit symptoms at low severity levels are similar to those of FCR, which vary from light through medium to dark brown, extending partially to completely down the fruitlet core. FCR from *Fusarium* sp. is usually a 'dry' type of rot (see Fig. 9.26). In Brazil, the symptom is not limited to a single infected fruitlet, as in typical FCR reported in other pineapple production areas. Fruit symptoms involve multiple fruitlets, with the infected area of the fruit surface appearing off-colour initially and later becoming sunken, with profuse pink sporulation and exudation of gum (Fig. 9.30). Gum exudation can be confused with the exudation from *Thecla* wounds (see Fig. 9.24; Laville, 1980).

In Brazil, the disease causes major losses in the three major cultivars, 'Perola', 'Jupi' and 'Smooth Cayenne' (Rohrbach, 1983). Levels of fruit infection can vary from 5 to 75% (Laville, 1980). Infection is thought to occur through open flowers, although major levels of disease also occur from inoculations to the developing inflorescence (Ventura *et al.*, 1981). Infection of the inflorescence and fruit also occurs from injuries caused by insects, particularly the bud moth, *T. basilides*. Once the developing fruit is infected, secondary infections can occur on the developing slips or suckers. The infected seed material is then distributed to new planting areas, thus infesting new sites. Soils can remain infested for several months. Spread within infested fields is primarily by insects but may also be by wind (Laville, 1980). Free conidia of *F. subglutinans* can survive for 6–13 weeks in soil, depending on moisture and temperature, with survival being highest in dry soils. Survival in pineapple tissue in soil is less than 10 months (Maffia, 1980). Optimum tempera-

Fig. 9.30. Pineapple fruit in Brazil showing fusariosis caused by *Fusarium subglutinans*.

tures for growth are 25°C, with a range of 5°C to 35°C (Camargo and Camargo, 1974).

Control of fusariosis is most effective by planting disease-free seed material and by controlling insects, particularly the bud moth (Laville, 1980). Fungicides, such as captafol at 700 g a.i. ha^{-1}, starting at differentiation through harvest at 20-day intervals, have given good control of the fruit-rot phase in Brazil (Bolkan *et al*., 1978).

Pink fruit

Pink disease can be found at very low levels in most pineapple production areas of the world (Rohrbach, 1983). However, economically significant epidemics are only known to occur in Hawaii, the Philippines and Taiwan. When epidemics occur in Hawaii and Taiwan, the highest incidences occur in February, March and April. In the Philippines, however, epidemics occur from August to September (Hine, 1976).

Pink disease of pineapple fruit is characterized by the typical symptom of brown to black discoloration of the fruit tissue when heated during the canning process. Depending on the bacterial strain and the severity of the disease, symptoms in uncooked fruit may be completely absent or may include extremely severe fruit translucence, light pinkish to brownish colour of the fruit cylinder, and/or a 'cantaloupe-like' odour (Rohrbach and Apt, 1986). *E. herbicola* in uncooked pineapple fruit is essentially symptomless and very difficult to detect. *G. oxydans* in uncooked fruit induces pinkish brown to dark brown discolorations and may have a 'cantaloupe-like' odour. *A. aceti* – more recently classified as *Acetobacter liquefaciens* (Gossele and Swings, 1986) in uncooked fruit with only a few fruitlets infected can be symptomless. However, in moderately to severely infected fruit (many fruitlets infected), symptoms range from pinkish brown to dark brown (Rohrbach and Pfeiffer, 1976a; Kontaxis and Hayward, 1978). The symptom is reported to be caused by the bacteria producing 2,5-diketogluconic acid, which reacts with amino acids to form brown to black pigments (Buddenhagen and Dull, 1967). Strains of the acetic acid bacteria, such as *A. liquefaciens,* have been reported to produce browning and rotting of apples and pears and to have been isolated from guava, mango and Surinam cherry (Gossele and Swings, 1986).

In contrast to the other fruit diseases, the economic significance of pink disease is the inability to detect diseased fruit prior to processing, with the result of brown to black slices in a sealed can. Thus, quality control during processing is critical to detection of low levels and management of diseased fruit in the cannery (Rohrbach and Apt, 1986). In fresh-fruit production, low levels of pink disease are not of major economic importance. However, when high incidences occur, with strains having symptoms prior to cooking, economic loss can occur.

Marbled fruit

Marbling disease is caused by the acetic acid bacteria *A. peroxydans* Visser 't Hooft and *E.*

herbicola var. *ananas* (Serrano) Dye. Marbling disease has been reported in essentially all pineapple production areas of the world (Rohrbach, 1983). However, epidemic levels occur only in the lowland tropics, where temperatures remain above 21–27°C during fruit development (Rohrbach and Apt, 1986). In production areas such as Thailand, where disease incidence is high, from 5 to 20% of the slices in the cannery will be marbled. In Thailand, the incidence and severity of marbling can be high enough in October and November to close down processing operations (K.G. Rohrbach, personal observations). In Hawaii, highest levels occur in April and May although the disease may occur at any time. Low fruit acid and brix are also associated with high levels of the disease.

The fruit disease of pineapple termed 'marbling' is represented in the literature by a wide range of symptoms. The most common symptom is a yellowish to reddish brown to very dark dull brown discoloration of the infected fruit tissue. Infected tissues generally become hardened, granular and brittle in texture, with colour variation in the form of speckling (Rohrbach and Apt, 1986). The disease may affect individual fruitlets but more typically affects a group of fruitlets or the entire fruit. Frequently, the speckled appearance will occur in vascular tissues in the core of the fruit. The diseases reported as bacterial fruitlet brown rot (Serrano, 1928) and fruitlet black rot (Barker, 1926) have generally been considered to be a variation of marbling. An additional symptom, termed 'brown and grey rot', has also been associated with marbling disease. The causal organism of brown and grey rot will also cause marbling symptoms. In general, much less is known about marbling disease than about pink disease.

Currently, no known controls of marbling exist. Differences in cultivar susceptibility have been noted, with the 'Smooth Cayenne' variety being moderately resistant (K.G. Rohrbach, unpublished results). When epidemics occur, infected fruit can be detected and excluded prior to going through the cannery by external appearance and a test to measure fruit firmness, such as sticking a knife into the fruit. If incidences are extremely high, all fruit must be discarded. In contrast to pink disease, marbled-fruit tissues can be discarded before being packing in cans.

Internal browning

Internal browning, also termed endogenous browning or black heart, is a physiological disorder of pineapple fruit. The disorder is of major significance in Australia, Taiwan, Kenya and South Africa, where fruit are grown and harvested at or near frost conditions (0–10°C). The disorder is also very important in the marketing of fresh fruit when refrigeration is used to extend shelf-life.

Internal browning is of economic importance only where fruit are grown under very cool conditions or are refrigerated for long periods through marketing channels prior to consumption (Paull and Rohrbach, 1985).

Internal browning is characterized initially by a small greyish translucent zone beginning at the base of the fruitlet (see Fig. 9.31) adjacent to the fruit core. This zone later darkens, becoming brown to black. When symptoms are severe, the entire internal fruit tissues are brown to black, thus giving rise to the name 'black heart' (Fig. 9.31; Paull and Rohrbach, 1982).

No organisms have ever been shown to be associated with the internal browning symptom. Internal browning is thought to occur from increased polyphenol oxidase activity (Teisson, 1979; Paull and Rohrbach, 1985). Low ascorbic acid levels have been associated with symptom expression (Paull and Rohrbach, 1985).

Symptoms may develop in fruit that has matured in the field at low temperatures in the range 5–10°C. Symptoms may also develop within 4 days of ambient temperatures following refrigeration at common commercial shipping temperatures of 7°C (Rohrbach and Apt, 1986).

Mites

Severe damage when fruit mature under drought conditions may cause death of the

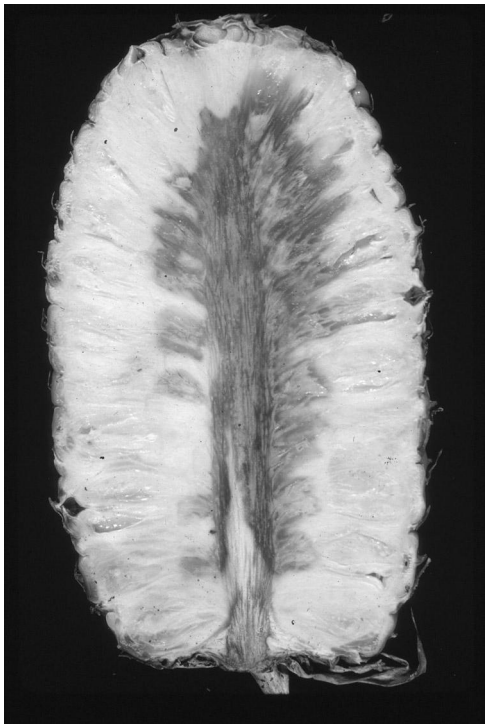

Fig. 9.31. Internal browning, a physiological disorder caused by chilling injury.

basal crown leaves, thereby affecting fresh-fruit quality and enhancing the potential for quarantine examinations (Rohrbach and Schmitt, 1994).

Scale

Normally, in Hawaii, pineapple scale is not a major problem in the field, probably because of scale parasites and predators. However, because of the quarantine requirement to have fruits insect-free, even low levels of pineapple scale at harvest may present quarantine problems.

Miscellaneous Fruit Diseases, Pests and Deformities

Numerous pineapple fruit diseases and blemishes of minor occurrence and importance have been noted and described, much of it in unpublished form. The minor importance of these symptoms and abnormalities results from their sporadic occurrence and lack of economic effects on pineapple production. Thus, little has been done to determine the cause and aetiology of these symptoms and abnormalities.

Yeasty fermentation

Yeasty fermentation is caused by the yeast species *Hanseniaspora valbyensis* (M. Okimoto, unpublished data) and can be a major problem in overripe fruits. A dry yeast rot has been attributed to *Candida intermedia* var. *alcoholophila* (M. Okimoto, unpublished data). Occasionally, the disease will occur in green fruit, having severe interfruitlet corking symptoms with associated fruit cracking (K.G. Rohrbach, personal observation). The disease has also been associated with high incidences of fruit sunburn (Lim, 1985). Losses can be minimized by reducing sunburn and harvesting fruit before they are overripe.

Glassy spoilage

Glassy spoilage is caused by infections with the yeast *C. guilliermondii* and may be associated with fruitlet core rots (M. Okimoto, unpublished data) caused by mixed infections of yeast and *Penicillium* or *Fusarium* species As with yeasty fermentation, losses can be minimized by harvesting before fruit are overripe.

Acetic souring

Acetic souring is caused by bacteria and is characterized by an offensive odour similar to that of a mixture of organic acids, including acetic acid. Juice of infected fruit may be very viscous and cloudy with bacteria. No controls are known.

Miscellaneous fruit rots

Fruit rots caused by *Aspergillus flavus*, *Botryodiplodia theobromae* and *Rhizopus oryzae*

or *Rhizopus stolonifer* have been reported as postharvest diseases (Snowdon, 1990). A fruit rot caused by *Hendersonula toruloidea* (Natt.) has been reported by Lim (1985) on the Mauritus cultivar. Green fruit rot caused by *Phytophthora* species occasionally causes large losses of lodged first-ratoon fruit in Australia under very wet conditions. These pathogens generally require some form of wounding for infection. Commercially, these diseases are of very minor importance.

Miscellaneous physiological fruit diseases

Woody fruit

Woody fruit is a disease of unknown cause. The disease is characterized by brown streaks distributed throughout the fruit tissue, which is very woody and hard in consistency. The disease is associated with certain clones of 'Smooth Cayenne' and therefore is assumed to be of genetic origin. Roguing at harvest is used to eliminate seed material from plants showing symptoms.

Sun scald and frost injury

Sun scald is characterized by a discoloration of the fruit shell, which ranges from yellow to tan or black on the side of the fruit exposed to the sun. The internal tissues are usually a pale grey colour, but, when severe, the affected area becomes sunken and desiccated. Fruits that fall into an exposed or reclining position are much more susceptible. On clear, calm days, temperatures of 50–54.4°C have been recorded in exposed fruit (K.G. Rohrbach, unpublished results). Where sun scald is a problem in summer months (e.g. Australia, South Africa, Taiwan and Brazil) straw, weeds or shredded paper may be used to cover the exposed side of the fruit for control (Lim, 1985). Sprays of a 4:1 mixture of talc and bentonite are used by larger growers in Australia to reduce incidence of injury.

Frost injury occurs occasionally in some areas in Australia. Symptoms are shell discoloration and cracking between the eyes.

Fasciation/multiple crowns

Multiple crowns (two or more) develop when young fruit are exposed to high temperatures early in the development stage. Because nothing is known about the stage of fruit development most susceptible to high temperatures, no controls are available. The problem is mainly important where fruit are to be sold fresh with the crowns attached. In Australia, multiple crowns are trimmed to one to improve appearance and to facilitate packing in boxes.

Fasciation is an abnormal development of the inflorescence and crown, resulting in a flattening of the upper part of the fruit with multiple crowns ranging from two to many. Fasciation has been associated with genetic and environmental conditions, although Py (1952) has indicated that the phenomenon is not hereditary. Cultivars such as the 'Smooth Cayenne' are less susceptible than the 'Singapore Spanish'. Within the 'Smooth Cayenne' cultivar, certain clones are much more susceptible than others.

Trephritid fruit flies

Prior to 1953 methyl bromide was used to treat pineapple imported into continental USA. Since then, it has been demonstrated that 'Smooth Cayenne' pineapple cultivars (low- and high-acid types, with at least 50% 'Smooth Cayenne' parentage) are not hosts for the tephritid fruit flies: Mediterranean fruit fly, *Ceratitis capitata* (Wiedermann), melon fly, *Dacus cucurbitae* (Coquillet), and the oriental fruit fly, *Dacus dorsalis* Hendel (Bartholomew and Paull, 1986).

Management of postharvest diseases and pests

Black rot is commercially managed by minimizing bruising of fruit during harvest and handling, by refrigeration and with chemicals. Fruit must be dipped in an appropriate fungicide within 6–12 h following harvest prior to packing and shipping (Rohrbach Phillips, 1990).

Internal-browning symptom development can be reduced by waxing with paraffin-polyethylene waxes at wax-to-water ratios of 1:4–9 (Rohrbach and Apt, 1986). Waxing has been shown to increase internal CO_2 concentrations, thereby lowering O_2 concentrations, which results in reduced polyphenol oxidase (Paull and Rohrbach, 1985).

The *Penicillium*-induced FCR, LP and IFC fruit diseases have been reduced by applications of endosulphan (3.35 kg a.i. ha^{-1} in 2338 l water) at forcing and 3 weeks following forcing. Reductions have been significant but only under low to moderate disease levels (Le Grice and Marr, 1970; Rohrbach *et al.*, 1981; Rohrbach and Apt, 1986). Fungicides, such as benomyl, have not been effective unless applied directly into the open heart as the inflorescence emerges (K.G. Rohrbach, unpublished results).

Control of typical FCR induced by *F. subglutinans* has not been demonstrated. Control of fusariosis is most effective by planting disease-free seed material and by controlling insects, particularly the bud moth (Laville, 1980). Hot-water treatment of seed material at 54°C for 90 min with benomyl at 50 g 100 l^{-1} is effective for disinfestation but will retard growth and kill up to 50% of the plants (Maffia, 1980). Fungicides, such as captafol, at 700 g a.i. ha^{-1}, starting at differentiation through harvest at 20-day intervals, have given good control of the fruit-rot phase in Brazil (Bolkan *et al.*, 1978). Resistance to fusariosis occurs in *Ananas* and *Pseudoananas* (Laville, 1980).

Scale can be controlled relatively easily by preharvest applications of an appropriate registered insecticide, taking into consideration last application to harvest residue restrictions.

Ratoon Crops

In general, control of weeds, insects (ants, mealybugs, scales), nematodes and diseases (root rots, fruit diseases) in ratoon crops is very much dependent on the efficiency of controls that were applied during the development of the plant crop. Postplant applications of nematocides (e.g. fenamiphos) following plant-crop harvest have not resulted in yield increases in Hawaii but have increased yields in Ivory Coast (Caswell *et al.*, 1990).

Integrated Pest Management

Environmental and food-safety concerns have focused attention on IPM. The concept of IPM is to employ several techniques simultaneously to solve specific pest and disease problems for the long term rather than in the short term. Success relies on an in-depth understanding of the pineapple production system and the ecology and biology of each pest or disease and associated organisms (e.g. vectors, natural enemies). Emphasis must be placed on the importance of each pest or disease from an economic, biological and ecological perspective (Pedigo, 2002). In order to evaluate the importance of the pest or disease, efficient techniques are needed to monitor changes in populations of pest and levels of diseases or pathogen populations. The changes must be correlated with yields and quality.

In most pineapple production systems throughout the world, mealybug wilt must be controlled by the management of ants and mealybugs. Severe infestation may have an impact on the production system and the final product in several ways. As a direct pest, feeding reduces plant growth, fruit quality and yield. The presence of mealybugs on fresh fruit may become a quarantine issue, as well as a quality issue when present in the canned product. The indirect effect and the most severe impact are the resulting mealybug wilt, with high rates of field infestation.

Ants play a major role in the impact of mealybugs and mealybug wilt on pineapple. Soil tillage during fallow eliminates essentially all in-field ants, and new infestations must move into the newly planted field from field border areas. The rate of establishment of permanent ant colonies and mealybug wilt is relatively slow (Beardsley *et al.*, 1982). When ants are controlled, the parasitoid *Anagyrus ananatis* Gahan (Fig. 9.32) and other biological control agents can maintain

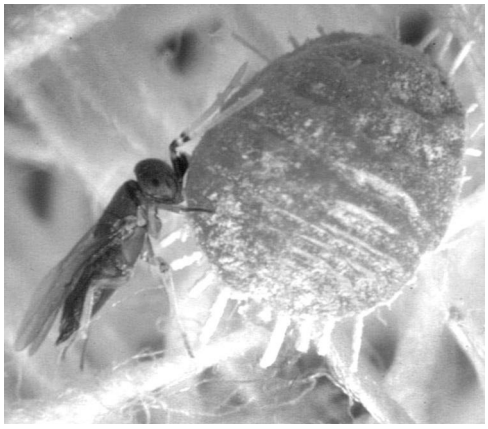

Fig. 9.32. The parasitoid *Anagyrus ananatis* on a pink pineapple mealybug, *Dysmiococcus brevipes*.

populations of the pink mealybug below damage thresholds in Hawaii. The use of Amdro® is efficacious, allowing natural biological control agents to function while reducing overall insecticide usage.

Techniques for monitoring ants, using trap stakes, have been developed (Fig. 9.33; Beardsley *et al*., 1982). Recommendations are to use trap stakes baited with peanut butter/soybean oil at intervals of 30 m (100 ft) along field borders of new plantings. Trapping must be done in late afternoon, with data being taken after darkness occurs. The first monitoring should start at 3 months following planting and be repeated at 3-month intervals thereafter. When ants are detected, they may be controlled with site-specific applications of ant baits or insecticides. Other monitoring techniques, such as pit-fall traps, honey-vial traps and pineapple-juice traps, have also been used. Threshold levels of ants have not been very well defined and the presence of any ants is considered problematic.

Populations of mealybugs have been monitored with sticky tape placed in the lower part of the pineapple plant (Fig. 9.34; M.W. Johnson, unpublished results). Relatively high levels of mealybug are required for mealybug wilt. Diagnosis of mealybug wilt virus-infected seed material can be done rapidly and inexpensively, using a tissue-blot immunoassay system (Hu *et al*., 1993), in order to establish virus-free plantings. Evaluation of the impact of virus-free plants on growth and yield has not been completed, but studies are under way (D. Sether, personal communication).

Reniform and root-knot nematode threshold levels at planting for pineapple production in Hawaii have not been well defined.

Fig. 9.33. Field sampling for ants using white stakes with the base painted with honey/water (50 : 50) or peanut butter/soybean oil and placed out from 3 to 6 p.m. and read at 7–10 p.m.

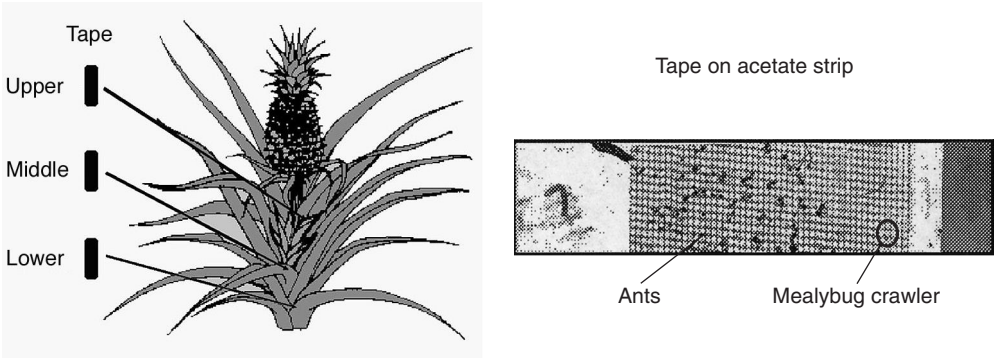

Fig. 9.34. Sampling technique for mealybugs using acetate strips with double-sided sticky tape placed on leaves in the middle and lower sections of the pineapple plant (M.W. Johnson, unpublished data).

Reniform nematode populations in soil stay low until 6–9 months following planting and then peak at 12 months (Sipes and Schmitt, 1994). The field history of nematode populations and their impacts on yield is important in nematode management.

Nematodes are currently managed primarily by soil fumigation and postplant nematocides. A clean fallow period is also used to reduce populations. Crop rotation was used in the early part of the century in Hawaii but has not generally been practised since the discovery of soil fumigants. Crop rotation has not been practical in recent years, because of the high cost of planting and maintaining (irrigation) the rotation crop, along with the inability to develop marketable rotation crops. Non-host cover crops, either within the growing crop or during fallow, have been studied with varying degrees of success (Caswell *et al.*, 1991). Cover crops may be feasible only in high-rainfall areas. Fumigation efficacy is influenced to a major degree by the soil-tillage practices prior to fumigation and soil moisture during tillage and at fumigation (Caswell and Apt, 1989). The use of plastic mulch reduces fumigant losses to the atmosphere, as well as reducing the amounts of herbicides required. Efficient nematode control integrates all the above strategies.

Phytophthora heart rot and root rots of pineapple are diseases limited to fine-textured, high-pH soils under wet environmental conditions. Control strategies involve improving surface and internal soil drainage. Raised planting beds have provided good control under wet conditions but poorer growth under dry conditions. Fosetyl aluminium and ridomil are very effective as preplant dips. Fosetyl aluminium also provides good heart-rot control as a foliar application at 3–6-month intervals and excellent control of *P. cinnamomi* root rot (Rohrbach and Schmitt, 1994). Resistant cultivars to both *P. cinnamomi* and *P. nicotianae* var. *parasitica* exist but are not commercially viable, due to low yields or poor fruit quality (Rohrbach and Schmitt, 1994).

Both pineapple butt and black rot are caused by the fungus *C. paradoxa.* The severity of the problem in fresh fruit is dependent on the degree of bruising or wounding during harvesting and packing, the level of inoculum on the fruit and the storage temperature during transportation and marketing. Currently, these diseases are controlled by dipping the crown or fruit in a fungicide prior to planting or shipping of the fruit (Cho *et al.*, 1977). Treatment must be done in 12 h or less from the time the crown or fruit is removed from the plant (Rohrbach and Phillips, 1990).

Inoculum levels on fruit at harvest vary according to the environmental conditions prior to harvest. The high correlation between moisture (rainfall duration) prior to harvest and disease following harvest has resulted in the name water rot. Storing seed material on the mother plants during dry weather, where there is good air circulation and minimal exposure to inoculum-infested

soil, provides excellent control. However, stored seed results in poor uniformity of early plant growth and can reduce crop yields. Planting fresh planting material results in more rapid uniform growth. Freshly removed seed material for immediate planting must be dipped in a fungicide within 12 h of removal. Currently, seed materials are dipped in triadimefon.

Black rot is commercially controlled in fresh fruit by minimizing bruising of fruit during harvest and handling, by refrigeration and with chemicals. Fruit must be dipped in a fungicide within 6–12 h following harvest prior to packing and shipping. Currently fruit can be dipped in triadimefon. The 'Red Spanish' cultivar is generally more resistant to *C. paradoxa* than 'Smooth Cayenne', but, due to low yields and poor quality, this is not an economically viable cultivar.

Pineapple scale only becomes a problem when the balance of biological control is upset, for example by the application of residual, broad-spectrum insecticides (Sakimura, 1966). Quantitative monitoring techniques have not been developed. While a monitoring technique has been developed for the tarsonemid mite (Fig. 9.35), correlation with the *Penicillium*-induced fruit diseases has not been well enough established to predict disease.

IPM for pineapple production systems has met with varying success and has not been broadly implemented for several reasons. First, less expensive alternatives are still available. The annual application of Amdro® for ant control in pineapple is much less expensive than the labour required for a detailed ongoing monitoring programme. As long as other alternatives are available, farmers will not learn and implement monitoring activities. Second, in Hawaii, the importation and development of biocontrols have essentially reached a standstill because of environmental concerns for non-target species. Until agriculture is forced by economic or regulatory incentives to implement IPM, traditional pest and disease strategies will be used. Thirdly, IPM does not generally reduce pest and disease levels low enough to meet quarantine requirements, thus requiring other pest- and disease-control strategies.

Fig. 9.35. Sampling for pineapple fruit mites by washing heart leaves in 70% ethanol. Samples can then be stored and counted.

In Hawaii, an IPM verification programme has been established, which was modelled after the national IPM protocol for potatoes. Multidisciplinary teams, including members from industry, research and extension, identify pests and diseases and recommend IPM practices. IPM protocols are developed based on establishing the best management approaches. Verification of producer practices is done by farm visits and review of records, in order to assign points in relation to each IPM protocol. High scores allow producers to use IPM as a marketing tool and to better educate farmers and consumers as to the value of products grown under IPM principles (A. Hara and R. Mau, personal communication).

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10 Postharvest Physiology, Handling and Storage of Pineapple

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Introduction

The first pineapple was reported to have been planted in Honolulu, Hawaii, in 1813 by Don Francisco de Paula y Marin (Collins, 1934). Fresh fruit were soon being sold to overwintering whaling ships visiting Hawaii. Between 20 August 1849 and 10 August 1850, 12,000 fruit were shipped from Lahaina, Maui, to California (Parsons, 1853). The condition of the fruit upon arrival is unknown. Shipments were also made in the 1890s to Australia, New Zealand, the US west coast Pacific ports and Canada. In 1906, a mail-order service existed in Hawaii that would send six fruit, each weighing about 6 lb, to New York by steamer and Wells Fargo Express for US$5.10 Now fresh fruit are shipped from Hawaii throughout the year, the largest amount being shipped during March, April and May, when deciduous fruits are less available. Similarly in other areas of world, pineapple producers are increasing their sales of fresh fruit. The ability to provide a year-round supply came when plant forcing was widely adopted; previously fruit availability was based on natural flowering.

Of the many pineapple cultivars, 'Smooth Cayenne' is the major commercial clone. Other cultivars are grown on a small scale (Brown, 1953; Collins, 1968; Samuels, 1970; Grazia *et al*., 1980), with many selected for specific localities (Collins, 1968; Chan, 1986; Cabot, 1987, 1989). 'Queen', 'Spanish', 'Pernambuco' and 'Mordilonus-Perolera-Maipure' are commonly grown for local fresh-fruit use. Cultivars of the 'Queen' group are widely available on European markets. Selections of 'Smooth Cayenne' and other cultivars have been made throughout the world, though they have not been well characterized. Though 'Smooth Cayenne' is the major cultivar worldwide, it has deficiencies as a fresh fruit. These deficiencies include high acidity, low ascorbic acid, sometimes poor flavour and a susceptibility to translucency. Cultivars better suited for fresh fruit and for specialized market requirements are being planted (Paull, 1992). This chapter follows from an earlier review (Paull, 1997) and incorporates more applied aspects of postharvest handling.

Fruit Development

Bract, calyx and ovary tissues have become fused within and between fruitlets during development to form the collective fruit

 The Pineapple: Botany, Production and Uses (eds D.P. Bartholomew, R.E. Paull and K.G. Rohrbach)

(Okimoto, 1948). Due to the fused nature of the tissue within a single fruitlet, the flesh of the fruit is not sterile but contains fungi, yeasts and bacteria (Rohrbach and Apt, 1986) though the population of microorganisms declines with fruit development (C.-C. Chen and R.E. Paull, unpublished results). No floral abscission occurs, so the withered style, stamens and petals can be found on a mature fruitlet. The large bract subtending each fruitlet is fleshy and widened at its base and bends over the flattened calyx surface, covering half of the fruitlet. Cell division is completed prior to anthesis and all further development is the result of cell enlargement (Okimoto, 1948). Fruit-development studies (Sideris and Krauss, 1938) have shown that fruit weight and its components (core, fruitlets, the collective flesh, fruit shell) increase in a continuous sigmoid fashion (Fig. 10.1A) once the inflorescence has been initiated (Gortner *et al.*, 1967). More recent data have confirmed the results of the earlier study (Singleton, 1965; Teisson, 1973). Fruit mass increases about 20-fold from the time of flowering until maturation (Singleton, 1965; Teisson and Pineau, 1982). The number of fruitlets comprising a fruit varies widely with plant condition and environmental conditions. A typical 'Smooth Cayenne' fruit has about 150 fruitlets, which produce a mature fruit weighing about 2.2 kg (Tay, 1977). Fruit dry-matter content can vary with the conditions prevailing during fruit development. While the crown probably has

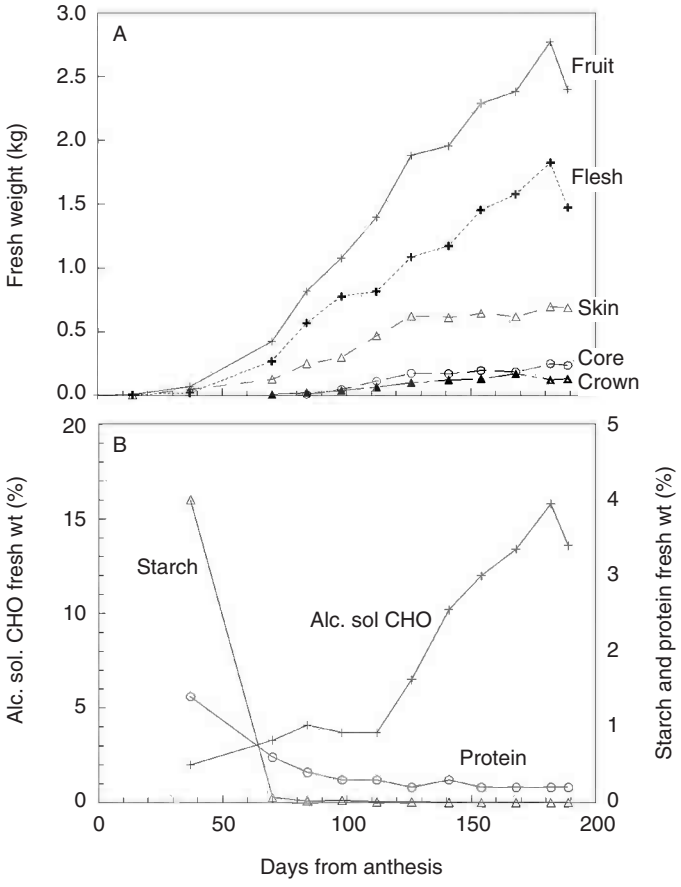

Fig. 10.1. Pineapple fruit growth and development (A) and changes in flesh starch, alcohol soluble carbohydrate (Alc. Sol. CHO) and protein (B) (after A. Hepton, 1995, personal communication).

no direct effect on the growth of the fruit (Senanayake and Gunasena, 1975; Chen, 1999), crown growth increases for about 30–45 days after fruit growth has commenced. Crown removal early in fruiting does not always lead to greater fruit weight. Crown size can be reduced by the plant growth regulator chloroflurenol when applied at the flowering stage (Dalldorf, 1981; Py *et al*., 1987); naphthalene acetic acid (NAA) and 2-(3-chlorophenoxy)-propionic acid (3-CPA) have also been used to reduce crown size (Bartholomew and Criley, 1983). Preliminary work also suggests that the crown may play a role in fruit translucency development (Paull and Reyes, 1996). Translucency is when the flesh has a water-soaked appearance.

Crown size is an aesthetic character of economic concern for packing and is generally part of the grading standard (Table 10.1). There does not appear to be a relation throughout the year between crown, fruit size and stem starch; the crown photoassimilates seem to be derived from its own photosynthesis (see Hepton, Chapter 6, this volume).

Under short day lengths and cool night temperatures, natural induction of inflorescence development occurs (see Malézieux *et al*., Chapter 5, and Hepton, Chapter 6, this volume). This precocious flowering disrupts harvest scheduling, increases the number of passes necessary to harvest a field and, if small plants are induced, leads to smaller fruit. Applying plant growth regulators is a possible approach to limiting environmental induction (see Bartholomew *et al*., Chapter 8, this volume), or transgenic plants with reduced environmental sensitivity may be produced.

Fruit Physiology

The half-yellow stage is regarded as ripe and is near the maximum fruit weight if still on the plant (Wardlaw, 1937). Fruit development (Fig. 10.1A) and composition changes (Fig. 10.1B) during growth have been reviewed (Gortner *et al*., 1967; Bartholomew and Paull, 1986; Py *et al*., 1987; Paull, 1993). The most marked changes in flesh composition occur in the 3–7 weeks prior to the half-yellow shell-colour stage (Dull *et al*., 1967; Dull, 1971; Tay, 1977; Teisson and Pineau, 1982; Chen and Paull, 1995). Just prior to the half-yellow stage, fruit translucency can start to develop, with this development continuing after harvest.

Senescence-related loss of membrane integrity leads to water-soaked, translucent flesh, which tends to be softer than non-translucent fruit. Gortner and Leeper (1969) have shown that amides, nitriles, simple esters and salts of phenoxy acids, naphthalene compounds, phenyl acid and trichlorophenoxyacetic acids can delay fruit

Table 10.1. United States fresh pineapple fruit standards. All grades have 10% limits as to defects, 5% as to serious damage, and 1% decay.

Standards	Varietal characteristics	Maturity	Freedom from	Slips and knobs	Crown-to-fruit length ratio
US Fancy	Similar	Mature, firm, dry, well-formed, well-developed eyes	Decay, sunburn, injury, bruising, well-cured butt	Single crown, no crown slips	Ratio less than 1.5, not less than 5″ in size
US No. 1	Similar	Mature, firm, dry, well-formed, well-developed eyes	Decay, sunburn, injury, bruising, fairly well-cured butt	< 5 crown slips	Ratio less than 2.0 and greater than 4″ in size
US No. 2	Similar	Mature, firm, dry, fairly well-formed	Free from serious decay, sunburn, injury, bruising	Crown slips	• Any ratio • Double crown

senescence. NAA and phenoxyacetic acid are the most effective in delaying shell yellowing when applied as brief postharvest dips (Gortner, 1969). These chemicals induce little change in total soluble solids (TSS), acidity, carotenoid pigments or vitamin C content; both chemicals are, however, phytotoxic to the crown. There are no marked changes in fruit texture during ripening. Water loss can lead to some reduction in fruit firmness.

Shell chlorophyll

Chlorophyll levels show little change until the final 10–15 days before full shell yellowing and then decline (Gortner, 1965; Py *et al*., 1987). Shell carotenoid pigments remain reasonably constant during this phase, declining only slightly before rising again as the fruit senesces. Flesh carotenoids increase during the final 10 days before the full-ripe stage (Gortner, 1965; Teisson and Pineau, 1982; Py *et al*., 1987). A similar decrease in shell chlorophyll and an increase in flesh carotenoids occur in harvested fruit (Dull *et al*., 1967; Chen and Paull, 1995).

Respiration

The non-climacteric pineapple fruit produces around 22 ml kg^{-1} h^{-1} of CO_2 at 23°C, with no dramatic respiratory change during ripening (Dull *et al*., 1967). Ethylene production increases during ripening, but has no pronounced peak. Exogenous ethylene application stimulates only respiration rate when there is some chlorophyll remaining in the shell, and may also open the crown leaf stomata. The absence of a peak in ethylene production and lack of a relationship of respiration with pronounced biochemical ripening changes support the conclusion of a non-climacteric pattern of development (Dull *et al*., 1967).

Organic acid metabolism

Juice pH declines from 3.9 to 3.7 as fruit approach the full-yellow stage (Teisson and Pineau, 1982) and increases as the fruit senesces, with titratable acidity showing the opposite trend (Gortner and Singleton, 1965; Teisson and Pineau, 1982; Chen and Paull, 1995). The flesh acidity increases distally from the central core (4 mEq 100 ml^{-1}) outwards to 10 mEq 100 ml^{-1} (Huet, 1958b), and a major portion (65–70%) of the total non-volatile acids occurs as free organic acids (Chan *et al*., 1973; Teisson and Combres, 1979). The two major non-volatile organic acids are citric and malic (Chan *et al*., 1973). Malic acid can vary from 18% to 30% of total acids in pineapple and does not vary markedly between the cool- and warm-season crops (Chan *et al*., 1973), but can fluctuate threefold with weather conditions that favour water evaporation (Gortner, 1963). Malic acid accumulates when sunlight and evapotranspiration are low (Singleton and Gortner, 1965). Citric acid (28–66% of total acids) is lower in 'Smooth Cayenne' fruit harvested in the warm season and tends to vary primarily with stage of fruit development (Gortner, 1963). Citric acid increases uniformly, with fruit development peaking before malic acid and before full ripeness. Fruit malic acid levels do not change after harvest or during and after storage (Chen and Paull, 1995). During storage at 7°C, citric acid increases about 25% and then declines slightly when fruit are held at 22.5°C. The citric acid content of unstored fruit does not change, though there is a slight decline in titratable acidity after harvest.

Ascorbic acid content varies significantly with the clone (Kerns *et al*., 1936; Singleton, 1955; Teisson and Combres, 1979) and increases with increasing solar radiation (Gortner and Singleton, 1965) and air temperature. Ascorbic acid is correlated with a clone's acidity (Hamner and Nightingale, 1946), does not contribute substantially to titratable acidity and is 25% higher near the surface of the fruit than near the core. Ascorbic acid levels can vary from 200 mg l^{-1} in 'Smooth Cayenne' to 710 mg l^{-1} in 'Spiny Guatemala' (Singleton, 1955). The level of fruit ascorbic acid at harvest has been negatively related to the intensity of internal-browning symptoms associated with postharvest chilling injury (Teisson and Combres, 1979; Paull and Rohrbach, 1982).

Internal browning is a minor problem if fruit ascorbic acid content is greater than 500 μM (Teisson and Combres, 1979).

Sugar metabolism

Sugar content plays an important role in the flavour characteristics and commercial assessment of pineapple fruit quality (Py *et al.*, 1987). TSS, mainly sugars, are often used as an indicator of fruit maturity and quality (Paull, 1993). TSS can vary by 40 g l^{-1} from the more mature, sweeter basal tissue to the crown end of the fruit (Sideris and Krauss, 1933a; Miller and Hall, 1953), and decline only slightly after harvest (Paull and Rohrbach, 1982; Chen and Paull, 1995). Starch is not accumulated as the fruit ripens (Dull, 1971), though it is high during early fruit growth (Fig. 10.1B), which could explain the absence of dramatic changes in TSS postharvest.

The major sugars in mature fruit are sucrose, glucose and fructose (Gawler, 1962) and the peak in sucrose concentration is attained at full-yellow stage and then declines. Fruit sugars continued to increase through to senescence, unless the fruit is harvested (Kelly, 1911). Chen (1999) showed that total soluble sugar content is low during fruit growth and composed mainly of glucose and fructose. Glucose is at a slightly higher concentration than fructose during the early stages of fruit development. Sucrose accumulated rapidly 6 weeks before commercial harvest (Lodh *et al.*, 1972; Py *et al.*, 1987) and ultimately exceeds the glucose and fructose concentration (Chen, 1999). Fructose and glucose continue to increase postharvest (Singleton and Gortner, 1965; Tay, 1977). In addition, sucrose accumulated more in the fruitlet than in the interfruitlet tissue until the last 2 weeks of fruit development, when sucrose accumulation rate in the interfruitlet tissue was greater than in the fruitlet (Chen, 1999).

Three sugar metabolic enzymes (sucrose synthase, sucrose phosphate synthase and invertase) are thought to control sugar accumulation by fruit tissue. The activity of sucrose synthase (SS) is high in younger pineapple fruit and declines to a very low level 6 weeks before harvest, while the activity of sucrose phosphate synthase is relatively low and constant throughout fruit development (Chen, 1999). The activities of acid, neutral and cell-wall invertases are high in the younger fruit and decline to low levels 6 weeks before harvest, when sucrose starts to accumulate. The activity of cell-wall invertase (CWI) does increase 4 weeks before harvest, mainly in fruitlet tissue, while the activities of neutral invertase (NI) and acid invertase (AI) remain low, concomitant with the accumulation of sucrose, indicating that these enzymes may be a prerequisite for sucrose accumulation in pineapple fruit flesh. The high activity of CWI, favouring apoplastic phloem unloading, may play a role in sugar accumulation in pineapple fruit flesh at the later stages of fruit development (Chen, 1999).

Fruit cell walls

The cell walls of pineapple fruit parenchyma are regarded as unlignified, but do contain esterified ferulic acid (Smith and Harris, 1995). Overall, the non-cellulosic walls are intermediate between the unlignified *Poaceae* and typical dicotyledon cell walls. Glucuronoarabinoxylans are the major component of the non-cellulose fraction. Xyloglucans, along with smaller amounts of pectic polysaccharides and glucomannans, are present. Pineapple juice contains predominantly galactomannans (Chenchin and Yamamoto, 1978) and no acid sugars are detected, suggesting little pectin hydrolysis during ripening. This juice neutral polysaccharide forms a gum on processing equipment, which is readily hydrolysed by commercial cellulase, hemicellulase and pectinase preparations (Chenchin *et al.*, 1984). Glucan (1→3, 1→4) linkages are absent, in contrast to *Poaceae* cell walls. Glucuroarabinoxylans have also been isolated from lignified cell walls of pineapple leaf (Bhaduri *et al.*, 1983; Jarvis *et al.*, 1988).

Volatiles

A wide range of volatiles (157 compounds) have been identified, including esters, lac-

tones, aldehydes, ketones, alcohols and a group of miscellaneous compounds (Dupaigne, 1970; Flath and Forrey, 1970; Flath, 1986; Takeoka *et al*., 1989; Umano *et al*., 1992). Esters constitute over 80% of total volatiles (Umano *et al*., 1992). Free and glycosidically bound constituents have been found, including 2-pentanol, 2-butoxyethanol, hexanoic acid, phenol, 4-hydroxybenzaldehyde, vanillin and syringaldehyde, as aglycons (Wu *et al*., 1991). Volatile esters increase both on the plant and after harvest (Flath, 1986). The volatiles vary with cultivar (Gray, 1953) and are higher in summer fruit, especially ethyl alcohol and ethyl acetate (Haagen-Smit *et al*., 1945; Silverstein, 1971). Translucent fruit are higher in ester content, such as ethyl acetate, which is very low in opaque fruit (Gray, 1953). Information on the importance of individual components to the fruit aroma and flavour is still lacking, though furaneol and ethyl-2-methylbutanoate are the two largest odour contributors (Takeoka *et al*., 1989).

Lipids and amino acids

Total lipids decline at maturity, as does squalene content, while phospholipid, total sterol and amino acid values increase (Selvaray *et al*., 1975). Free amino acids in the juice are at a minimum at the middle of fruit growth (Gortner and Singleton, 1965). The exception is free methionine, found at low levels until the onset of ripening, when it increases to 0.7 mM at senescence.

Phenols

The phenolic acids (*p*-coumaric, ferulic and sinapic) have been tentatively identified in pineapple fruit. These acids, except sinapic, are in fruit showing internal browning and are the substrate for polyphenol oxidase activity (van Lelyveld and de Bruyn, 1977).

Enzymes

Peroxidase activity falls steadily during fruit development (Gortner and Singleton, 1965), reaching a minimum of one-third the initial value during ripening. Acid peroxidase (pH optimum 5.0) does not appear to be related to chilling-injury symptom development (Teisson, 1977), though it does decline during storage (Teisson and Martin-Prevel, 1979). Some purification of the two chilling-related enzymes, peroxidase and polyphenol oxidase (PPO), has been accomplished (Teisson, 1977).

No ascorbic acid oxidase was detected in one report (van Lelyveld and de Bruyn, 1977); however, ammonium sulphate-precipitated protein has been shown to have ascorbic acid oxidase that has a high pH optimum (> 8) and no activity below pH 6.0 (Teisson, 1977). These different assay conditions may explain the published discrepancies. The PPO has optimum pH near 5.0 and a temperature optimum near 45°C (Teisson, 1977). Das *et al*. (1997) found three PPO isoforms, with the major isoform being a tetramer of identical subunits (*c*. 25 kDa) and having an optimum activity between pH 6 and 7. The difference in pH may be due to the different extraction methods used or different isoforms. The PPO is stable to heat when extracted, but loses over 50% of its activity following 20 min exposure to 60°C *in vivo* (Teisson, 1977), and thiols and bisulphite inhibit activity. Catalase and indole acetic acid oxidase have also been detected, but changes in activity during ripening or storage have not been reported. Indole acid acid oxidase has a pH optimum of 3.5, which is at a variance with that in other fruit (Teisson, 1977).

Acetone powders of pineapple stem extracts contain the proteinase bromelain and a family of polypeptide inhibitors of this enzyme (Reddy *et al*., 1975). Proteinase activity appears abruptly after flowering, remains high during fruit development (Gortner and Singleton, 1965) and declines during ripening (Gortner and Singleton, 1965; Lodh *et al*., 1972). The major cysteine proteinase is fruit bromelain (EC 3.4.22.33), a non-glycosylated proteinase that is immunologically distinct from the glycosylated stem bromelain (EC 3.4.22.32) (Rowan *et al*., 1990). Fruit bromelain has an estimated molecular weight of between 23 and 31 kDa by different laboratories (Yamada *et al*., 1976; Ota *et al*., 1985;

Rowan *et al*., 1990). The fruit bromelain is an acidic protein and its isoelectric point (pI) is 4.6, different from the basic stem bromelain, the pI of which is 9.6 (Yamada *et al*., 1976). The amino-terminal end of the fruit bromelain, has an additional alanine (Yamada *et al*., 1976). The sequence around the reactive cysteine is the same. Fruit bromelain has a 20% cross-reactivity with anti-stem bromelain (Sasaki *et al*., 1973).

Fruit Harvesting and Handling

Quality criteria

A definition of pineapple fruit quality often refers to the sum of those characteristics of a fruit that make it most palatable and therefore desirable to consumers (Singleton, 1955; Paull, 1993). However, this definition does not allow us to measure such a quality standard; the standard varies with consumer tastes and with ethnicity and may be related to price paid. If multiple fruit-quality criteria (Table 10.2) were measured, the difficulty is how to sum the criteria and what normal range of variation would be used in the application of this scale.

Quality criteria used have been appearance (size, condition, shape), colour (shell and flesh), taste (sugars, acids), aroma, flesh translucency, texture and fibre content (Table 10.2). Skin colour is the most common measure of physiological maturity (Plate 34) and consumer expectations of quality (Dull, 1971). For some consumers, food value and vitamin content are also considerations. The changes in these parameters during pineapple fruit growth and development have been summarized (Gortner *et al*., 1967) and these data indicate the complexity of the changes that occur. For fruit-quality purposes, sugars are estimated as TSS by refractometry as percentage (g 100 ml^{-1} juice) sugars or as Brix. Problems soon arise in applying these criteria; TSS-to-acidity ratio is often used as a measure of flavour, though acid variation has a greater impact on the ratio than on TSS. A 20% TSS with 1% acidity will not taste the same as a 10% TSS with 0.5% acidity.

In pineapple, the problem of TSS and acidity is compounded by the effect of cultivars, season, maturity stage at harvest, position in the fruit and fruit-development conditions. The ascorbic acid content in 'Smooth Cayenne' varies from 130 mg l^{-1} at the base of the fruit to 280 mg l^{-1} at the less mature top part of the fruit; a similar variation occurs for titratable acidity (TA) (Singleton, 1955). TSS shows the opposite trend, having 19% TSS at the base and 15% at

Table 10.2. Subjective rating used for fresh pineapple fruit.

Criteria	Scale	Description
Shell colour	0–6	Immature green to overripe. 0–12%, 13–37%, 38–62%, 63–87%, 88–100% yellow eyes
Shell appearance	1–3	Brown or black discoloration to normal flesh, glossy
Crown	1–3	Dry, limp, brown to turgid, normal colour and fresh
Whole-fruit texture	1–3	Soft to firm: feel of fruit
Flesh texture	1–3	Limp to firm, crisp or fibrous texture
Translucency (slice)	1–5	Opaque to fully translucent
Translucency ($\frac{1}{3}$ from base)	1–4	Opaque to full translucent
Cylinder (vertical)		
Diseases and disorders		Number affected fruit and severity
Flavour	1–3	Fermented, bitter after-taste Very high acid, very high esters, very bland Normal

the top. While the TSS/acidity ratio may be constant after maturity, both TSS and acidity decline with increasing shell colour from about the 30% yellow shell-colour stage (Tay, 1977). Seasonal variation in sugar and acid levels can be significant: acid levels are higher during cool season and sugars (TSS) are lower. The reverse occurs in the warm season (Fig. 10.2).

Flesh TSS was reported as having the highest correlation with taste-panel eating quality ($R^2 = 0.70$, $P < 0.01$) and to be the most suitable year-round index (Smith, 1988a). The TSS/acidity ratio, juice pH and acidity were similarly suggested to be poorly correlated with eating quality (Smith, 1988a); however, the ranges in fruit acidity and TSS for the pooled data obtained from different growers in this study make interpretation difficult. For example, in one of the experiments the pooled results for TSS varied from 7.5 to 21.3 and eating quality from 1.5 to 7.6 (nine-step scale); these values exceeded the range of the pooled means used for the regression. In an earlier study, Sideris and Krauss (1934) found that fruit which had a sweetness index (TSS/% citric acid) greater than 19 was regarded as sweet and less acid by taste (Fig. 10.3). A sweetness index (TSS/acidity) of from 20 to 40 was recommended by Soler (1992a); Smith's (1988a) data on fruit TSS/acidity ratio ranged from 8 to 23. Commercially, the TSS/acidity ratio is regarded as the most reliable measure of fruit flavour.

Specific gravity (SG) may be a more useful intact-fruit grading index for eating quality (Smith, 1988b) than skin colour ($R^2 = 0.28$ versus 0.14). However, SG varies with season and geographical location of production (Singleton, 1945) and cultivar. Translucency correlates with SG but is not a good indicator of eating quality (Smith, 1988a), though previous results (Bowden, 1967) had recommended it as an index of ripeness. Palatability or eating quality reaches a maximum at the 50–60% translucent fruit stage and then declines to being less palatable than 30% translucent fruit at the 70% translucent stage (Bowden, 1969). This unpalatability may be related in part to fermentation in stored highly translucent fruit.

Fruit size and quality

Fruit size can be controlled by a number of agronomic methods (see Hepton, Chapter 6, this volume). Fruit size is set by plant size at forcing, as plant size influences the number

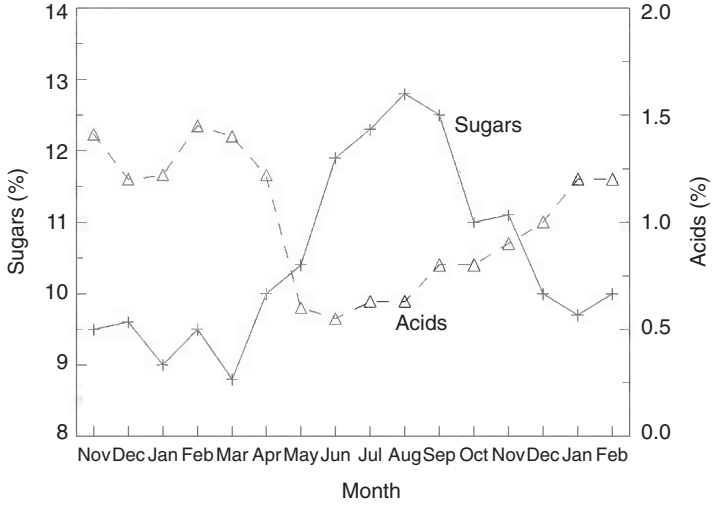

Fig. 10.2. Variation in sugar and acid percentage of mature fruit harvested at different times of the year (from Sideris and Krauss, 1934).

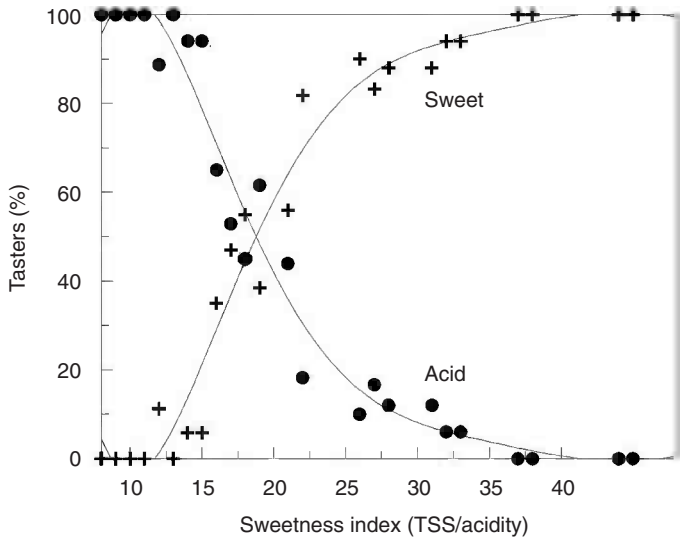

Fig. 10.3. The percentage of tasters who ranked fruit as sweet or acid against an index of sweetness (TSS/% citric acid) for a range of pineapple fruit (redrawn from Sideris and Krauss, 1934).

of florets (eyes) per fruit developed (see Hepton, Chapter 6, this volume). Plant size can be represented as plant weight, 'D'-leaf weight or the number of leaves (van Overbeek, 1946; Py *et al*., 1987; Malézieux, 1993). The larger the stump, the greater the number of florets possible. As a rule of thumb for 'Smooth Cayenne', each 1 kg of plant weight at forcing gives 1 kg of harvestable fruit. Cultivars will influence the relationship (Fig. 10.4) between plant weight at forcing and harvestable fruit weight (Chan and Lee, 2000). Some adjustment can be made in final fruit weight by increasing individual eye weight, initial weight of planting material, plant density and fertilization, especially nitrogen. However, too much nitrogen fertilization can lead to an increase in the number of fruit with double crowns and percentage of plants with collar of slips. Fruit size shows an inverse relationship to planting density, with about 45.4 g reduction in fruit weight for each 400 plants ha^{-1} increase above 7000 plants ha^{-1} (Sanford, 1963). Each 5 cm increase in spacing between 20 and 40 cm increases the fruit weight by about 5% and reduces the number of slips on the plant. The nearer that forcing is done to the natural differentiation, the larger the plant and the larger the fruit produced. Thus smaller fruit can be obtained by forcing earlier.

In the 'Smooth Cayenne' cultivar, nitrogen fertilizer tends to decrease fruit acidity while increasing fruit weight, fruit translucency in winter fruit and susceptibility of harvested fruit to chilling injury. Fruit chilling-injury intensity is reduced by potassium fertilization, especially when supplied as the chloride (Teisson *et al*., 1979). Magnesium fertilization does not significantly influence fruit acidity, while high magnesium application led to a significant decline in fruit TSS (Sanford, 1963). Potassium fertilization has no effect on TSS or slightly increases it. Other nutrients – calcium, phosphorus and micronutrients – have little effect on fruit quality and chilling sensitivity.

A temperature increase from 25 to 27°C over 5 months before harvest is related to a decrease in acidity from 12 to 7 mEq 100 ml^{-1} of juice (Huet, 1958a). Sunlight can also cause a similar decline in acidity (Lacoeuilhe, 1978). An inverse relationship is found between evapotranspiration in the 1–2 weeks before harvest and malic acid content (Gortner, 1963), while citric acid levels are little affected and more related to fruit development. There is a lag of about 1 week

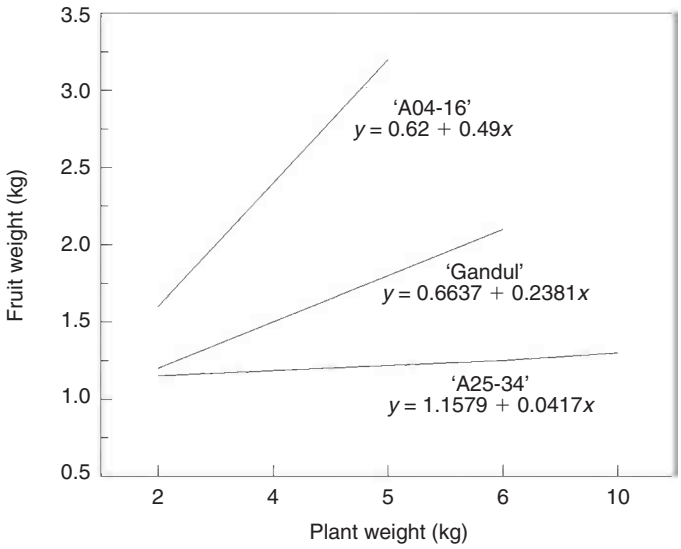

Fig. 10.4. Interaction between cultivars and plant weight and fruit weight at harvest (from Chan and Lee, 2000). Early-fruiting F1 hybrids ('Spanish' × 'Smooth Cayenne') were compared with 'Smooth Cayenne' ('Gandul').

between the increase in evaporation (sunlight) and the decrease in malic acid content.

In addition to the decrease in fruit weight with increasing planting density, there is also a decline in translucency, which may be related to light competition and fruit photosynthate supply (Chen and Paull, 2000). Planting density has little effect on fruit TSS or acidity, though they tended to be slightly higher (Sanford, 1963). Fruit esters do tend to decrease in fruit grown at higher planting densities. Though probably unrelated to density, ratoon crops tend to have smaller fruit with higher sugars, less acid and more flavour.

Fruit availability

Commercially, in favourable climates, planting, forcing and harvesting occur throughout the year. Some adjustment in area planted per month is made to allow for lower fruit demand in some months of the year. Low fruit production may be desirable in the months when there is strong competition from temperate fruits. When planting throughout the year, days from planting to forcing to first flower and first flower to harvest will vary at different times of the year. The variation is relatively small near the equator with near-constant average temperatures. As production moves away from the equator, adjustments in planting date and forcing date need to be made to ensure harvestable fruit at a certain time of the year (Fig. 10.5).

Accurate estimates of harvest date improve labour scheduling and fresh-fruit marketing. The first red centre at the plant apex (red bud) occurs 38–72 days after flower induction, the first time from opening of the last flower on a fruit takes from 19 to 28 days and the time from last flower to ripe fruit is 88–109 days. The total period from forcing to harvest ranges from 155 to nearly 300 days (see Hepton, Chapter 6, this volume). Near the equator (5°28′N), days from forcing to harvest range from about 150 to 175 days, with an average of 161 days (Fig. 10.5). At 100 m elevation on Maui (20°83′N) it takes 187 days, and at 800 m 242 days are required (Malézieux *et al.*, 1994).

Models to predict harvest date of 'Smooth Cayenne' have used hourly air-temperature data – a heat-unit model (Fleisch and Bartholomew, 1987) – and daily minimum and maximum air temperatures (Fleisch,

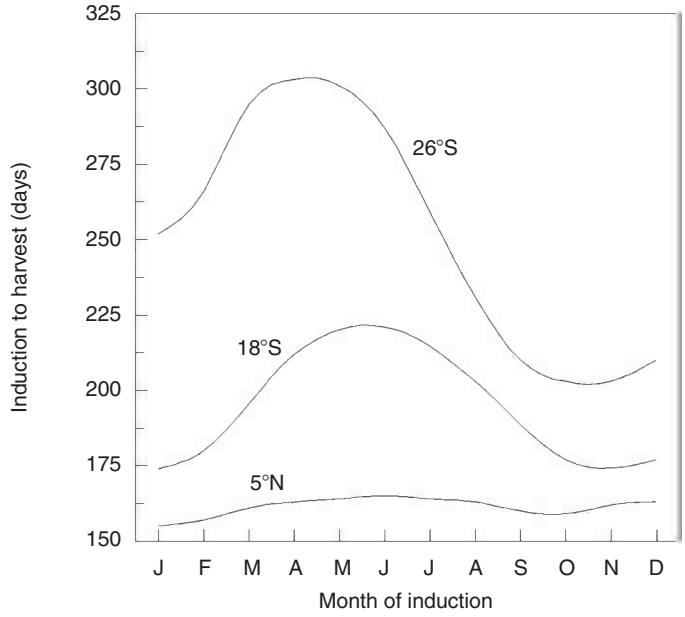

Fig. 10.5. Effect of latitude as an indicator of solar radiation and temperature on the time from forcing to harvest for 'Smooth Cayenne'; 26°S is Nambour, Australia, changed to northern hemisphere seasonal pattern, 18°S is Madagascar and 5°N is Ivory Coast (from Nakasone and Paull, 1998).

1988). The latter model is less accurate at low elevation on Maui and a poor predictor in Côte d'Ivoire and Queensland (Malézieux *et al.*, 1994). A model based upon daily minimum and maximum temperature with fruit development separated into two phases – forcing to first flower and first flower to harvest – was more accurate (see Bartholomew *et al.*, Chapter 8, this volume), giving mean errors of from 5 to 12 days. This model takes into account fruit temperature and not just air temperature. Other predictors of peak harvest in Hawaii have been based upon the juice optical rotation changing from negative to positive as sucrose accumulation begins, plus 53 days for a plant crop and 67 days for the ratoon crops. Alternatively, juice pH is measured for at least 4 weeks and extrapolated to a pH value of 3.54 for the plant crop and 3.1 for the ratoon crop, plus 28 days (Dull, 1960).

Preparation for harvest

Ethephon is used by growers 48 h or more before harvest to accelerate shell degreening and foster 'ripening' (Poignant, 1971; Crochon *et al.*, 1981). This accelerated shell degreening is due to the destruction of chlorophyll, giving the shell a more uniform yellow colour. The application of ethephon should occur just as natural shell yellowing begins, to ensure good fruit quality. If applied too early, the fruit may have 10% more acid and about 5% less sugar than non-ethephon-treated controls (Crochon *et al.*, 1981). Crochon *et al.* (1981) and Smith (1991) found variable effects of ethephon treatment on eating quality and this may be related to the acceleration of senescence. This variation depends upon the stage of fruit maturity (Soler, 1992a), how soon ethephon is applied prior to harvest (Smith, 1991) and the environmental conditions when applied (Soler, 1992b). Failure to apply ethephon uniformly on the fruit can also lead to irregular degreening. Crown damage can occur (Soler, 1992a) and the shell of more translucent fruit is more sensitive to ethylene and degreens more rapidly than less translucent fruit (Soler, 1992b).

The advantage of preharvest ethephon treatment is that fruit yellow (shell degreens)

more uniformly in the carton than untreated fruit, hence presenting a better overall carton appearance. There may be a minor acceleration of senescence and possibly faster loss of crown condition.

Fruit maturity and quality at harvest

Fruit maturity is evaluated on the extent of fruit 'eye' flatness and shell yellowing (Paull, 1993). Consumers similarly judge fruit quality by shell colour and aroma. A minimum of 12% TSS is required for fresh fruit in Hawaii (Anon., 1968), while others have suggested 14% (Smith, 1988b; Soler, 1992a). The TSS determined by refractive index needs to be adjusted for acidity to arrive at sugar percentage. The formula is: sugar (%) = TSS (% refractive index) − 0.192 (ml of 1 M NaOH to neutralize 100 ml juice). This formula applies generally, except for very translucent or overripe fruit. A rule-of-thumb value to obtain actual sugar content is to multiply the refractive index value by 0.85. This 0.85 factor may vary from 0.8 to 0.88 in opaque fruit and 0.86 to 0.96 in translucent fruit (Sideris and Krauss, 1933). Fruit TSS could also be determined by near-infrared spectroscopy (Shiina *et al*., 1993; Guthrie and Walsh, 1997) to within 1% TSS. A sugar-to-acid ratio of 20 : 40 is recommended in older literature, while Soler (1992a) recommended 14 : 20; both are lower than that recommended for the canned product (30 : 50) (Sideris and Krauss, 1934). However, extremely high or low values can lead to an insipid flavour.

The full-yellow fruit of 'Smooth Cayenne' are unsuitable for transporting to distant markets because they have a short shelf-life. Therefore less mature fruit are selected (Akamine, 1963; Cancel, 1974). Immature fruit are not shipped, since they do not develop good flavour, have low TSS and are more prone to chilling injury (Rohrbach and Paull, 1982). Immature fruit, if held at 20°C, improve in eating quality with time, approaching the quality of green mature fruit that do not change in eating quality after harvest (Smith, 1993). The same author found that one-quarter-ripe fruit maintained eating quality for up to 15 days at 20°C.

Harvesting

Pineapple is hand-harvested, with pickers being directed as to stage or stages of shell colour required (Plate 34). Picking early in the morning and protection of harvested fruit from the sun can reduce the heat load at cooling. In Hawaii, fruit are selected, broken from the peduncle by pickers and placed on a conveyor belt running on a boom to transfer the fruit to truck field bins or to be field-packed (Fig. 10.6). If packed at a central packing shed, the fruit is placed in the bin crown down by hand to avoid injury. Field-packed fruit show significantly less fruit bruising and crown injury. When the field bin with fruit arrives at the packing shed, fruit may be unloaded by hand, by submerging the field bin in water or by allowing the fruit to slide out of the field bin into water. Fruit with high translucency ('sinkers') are separated at this step. The sinkers are highly translucent fruit that are very fragile and have poor shelf-life. High translucency is also associated with bacterial and yeasty fermentation and acetic souring during handling, shipping and marketing. Adjusting the SG of the dump water with salt can be used to grade fruit as to translucency percentage. The water in the dump tank needs to be chlorinated and replaced frequently to prevent a build-up of disease organisms.

Care is taken to avoid damage to the crown leaves. Gibberellic acid can help retain crown condition during storage (Liu, 1986), though it is not approved in the USA for postharvest use.

Fruit bruising

Fruit bruising is a major problem during harvesting and packing (Plate 35). The bruised area leads to leakage of cell contents and provides openings for saprophytes and disease organisms. Bruising has been reported in 14% of inspected shipments arriving in New York (Cappellini *et al*., 1988). Translucent fruit are highly susceptible to bruising, and leaking of rupture cellular contents is common in bruised translucent fruit. The bruised flesh appears slightly straw-

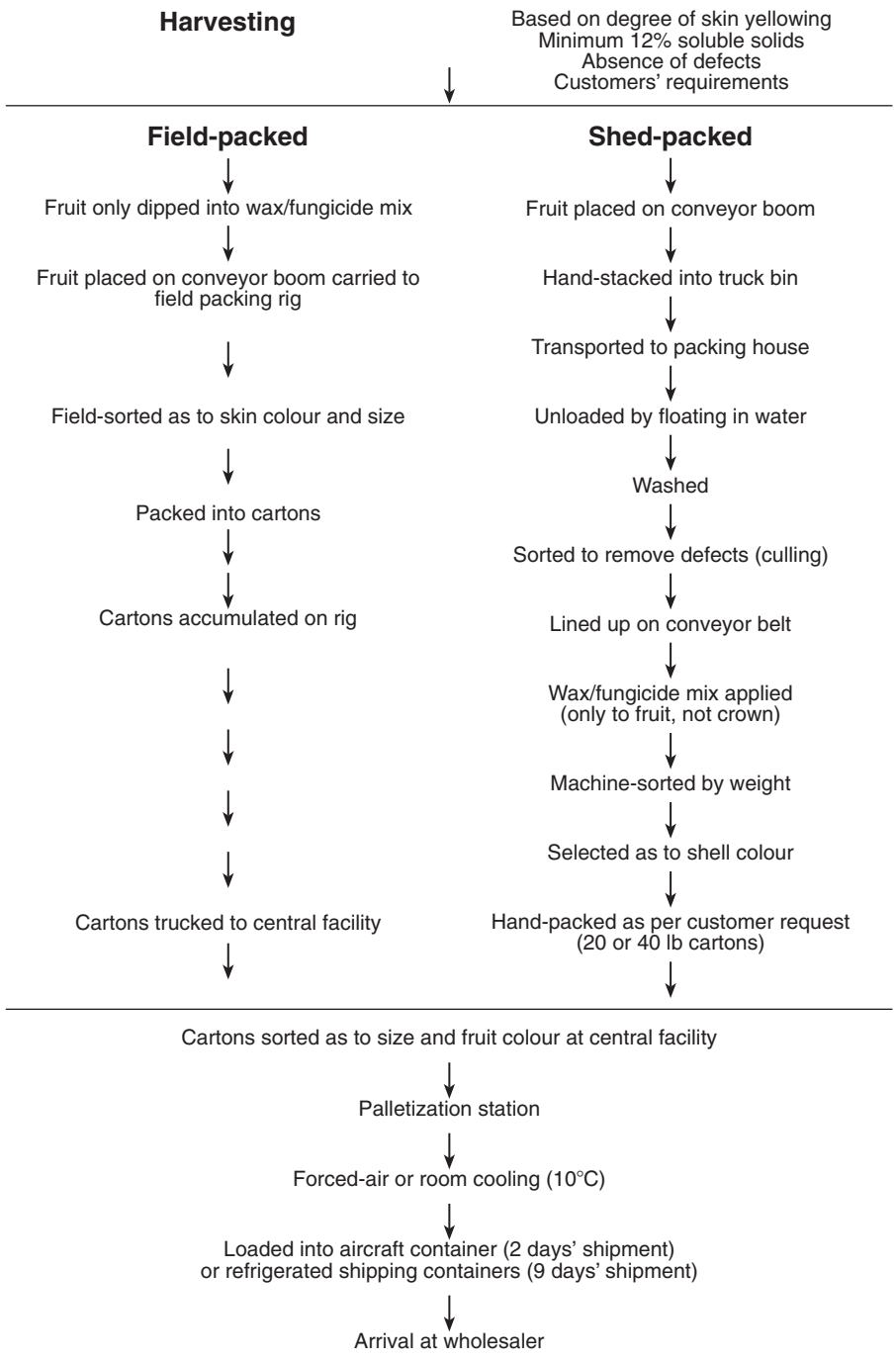

Fig. 10.6. A flow diagram of the postharvest handling system for fresh pineapples. In Hawaii, pineapples are required to have a minimum of 12% total soluble solids (from Anon., 1968).

coloured and becomes lead-grey with time (Keetch, 1978). A bruising test based on absorption-spectral changes in carotenoid extracted in alcohol : petroleum ether (1 : 1, 95% ethanol : petroleum ether, 60–110°C) has been developed, though it is not used commercially. The changes in carotenoids are associated with isomerization of the carotenoids at 466 and 425 nm (Singleton *et al*., 1961), caused by the release of acids from bruised cells (Gortner and Singleton, 1961).

A 30 cm drop is able to cause some impact damage (Singleton, 1958; Singleton *et al*., 1961). This injury is normally confined to the impact side of the fruit. Some estimates have been made of the impacts experienced during the unloading and grading of pineapple (Timm and Brown, 1991). The high impacts most often occur after the fruit are moved from the water in the dump tank on to inspection and singulator rollers; these rollers are made of steel or hard plastic and are not padded. The drop into the sizer cups or collection conveyors, which are padded, is half the force of that of drops on to the rollers (115 versus 55G).

One approach that significantly reduces harvest- and central packing-shed-related bruising is field-packing. Field-packing can reduce bruising injury to a quarter of shed-packing operations.

Postharvest fungicides and waxing

Hawaiian pineapples are commercially treated with a fungicide in a dip or spray application to control postharvest fruit rot, caused by the fungus *Chalara paradoxa (Ceratocystis paradoxa* (de Cynes) Moreau) (see Rohrbach and Johnson, Chapter 9, this volume).

A wax, frequently containing polyethylene/paraffin or carnauba/paraffin-based, may also be applied to the fruit with the fungicide (Plate 36). The major advantage of waxing is the reduction of the internal-browning symptoms of chilling injury. Waxing also reduces postharvest water loss and improves fruit appearance (Paull and Rohrbach, 1985). There is no worldwide uniformity in acceptance of wax components, so importing-country restrictions need to be considered. If the wax injures the crown leaves, only the fruit body is waxed.

Controlled- and modified-atmosphere storage

As with other non-climacteric fruit, controlled atmospheres via decreased oxygen levels or increased carbon dioxide have shown only minimal effectiveness in extending pineapple shelf-life (Akamine and Goo, 1971). The fruit waxes currently used in Hawaii generate higher internal concentrations of carbon dioxide (5%) and reduced oxygen tensions (Paull and Rohrbach, 1982). This suggests that some beneficial effect might be gained from controlled atmosphere (4% oxygen) treatments in reducing chilling-injury symptom development. Low oxygen (2–12%) has, however, been shown to enhance water loss from the crown leaves. There is no published work on lower oxygen levels with or without various controlled carbon dioxide concentrations.

Cellophane and polyethylene bags have been tested on numerous occasions to extend postharvest life (Pineapple Research Institute (PRI), 1962/63; Paull and Rohrbach, 1982, 1985). Both types of bags delay shell degreening when compared with unbagged fruit. Polyethylene bagging is objectionable because of the condensation problem, which leads to mould development, while cellophane bags allow moisture vapour exchange and the crown especially tends to dry out. Additional problems with all bags are the development of off-flavours and the difficulty of avoiding puncturing the bag with the crown leaves. An overwrap on the carton overcomes the puncturing problem but leads to problems in market inspection, and the wrap would need to allow some gas exchange to prevent excessive CO_2 build-up, which apparently leads to off-flavours.

Postharvest degreening of shell

Treating mature green pineapple fruit with ethylene postharvest leads to shell degreen-

ing occurring in *c*. 40% of the time required if fruit are left on the plant (Singleton, 1957a). Postharvest use of ethephon has been tested in the Ivory Coast (Poignant, 1971; Crochon *et al*., 1981), Hawaii (R.E. Paull, 1985, unpublished results) and Australia (Smith, 1991). Treated fruit show uniform skin degreening; however, shelf-life is shortened (R.E. Paull, 1985, unpublished results; Smith, 1991). Ethephon can be successfully incorporated into the fruit wax (R.E. Paull, 1985, unpublished results). The ability to apply ethephon with the wax is useful, as waxing delays fruit degreening. In the USA, the absence of registration for ethephon's use postharvest precludes its use. The need to degreen is related to the consumer's perception that a ripe pineapple must have a yellow skin. Exposing waxed fruit to red light during storage at 8°C also accelerates the rate of shell degreening upon return to ambient temperature (R.E. Paull, 1985, unpublished results). The degree of flesh translucency development postharvest is also less than that if the fruit is left on the plant to develop a fully yellow skin. Ethylene treatment has no significant effect on flesh TSS or acidity.

Fruit grading

The fruit to be packed needs to be mature, firm, well formed, free of defects, with flat eyes and a minimum TSS of 12% in Hawaii (Anon., 1968). Fruit are graded based upon recognized appearance characteristics: degree of skin coloration, size (weight), absence of defects and diseases and other market needs before packing (Table 10.1). Crown size is a crucial grade component (Plate 37), with a minimum size and a ratio of crown to fruit length of 0.33–1.5 for the higher grades. Crowns developed during the summer in Hawaii tend to be larger and may require gouging at harvest to meet the standard. This gouging leaves a wound for possible pathogen entry and degrades overall appearance. Gouging 2 months before harvest, avoiding visible scarring, is also practised to limit crown growth (Soler, 1992a).

Packaging

Fruit are normally packed into cartons of two different sizes. A large carton (20 kg) containing 10–16 fruit for surface or air shipment and a smaller carton (10 kg) for air shipment with five or six fruit. Tourist packs of two to four fruit are also prepared. Absorbent pads are used at the bottom of the carton and between layers if fruit are alternated horizontally within the carton. In other packs, fruit are placed vertically.

Postharvest storage

Temperatures in the range 7.5–12°C are recommended for storage, with relative humidities of 70–95%; the higher humidities significantly reduce water loss (Paull, 1997). The more recent recommendation is for 90–95% relative humidity. At a temperature of 0–4°C, the fruit may be stored for weeks, but upon removal, the fruit fails to continue ripening and shows severe chilling injury (CI).

Quarter-yellow fruit at harvest gain about 1 additional week's storage for every 6°C decrease in storage temperature (Dull, 1971). Half-ripe 'Smooth Cayenne' fruit can be held for about 10 days at 7.5–12.5°C and still have about a week of shelf-life (Fig. 10.6), with no chilling-induced internal browning. The maximum storage life at 7°C is about 4 weeks (Paull and Rohrbach, 1985); however, when removed to ambient conditions, CI-induced internal browning develops within 2–3 days. CI symptom development is more rapid at 20–25°C. Storage at 7.5–12.5°C does not generally lead to dramatic changes in acidity, though both sugars and ascorbic acid may decline (Singleton, 1957b; Paull and Rohrbach, 1982).

Postharvest chilling injury

CI symptoms may be caused by preharvest or postharvest exposure to temperatures less than 10–12°C (Akamine *et al*., 1975; Keetch and Balldorf, 1979). The symptoms develop when the fruit is returned from chilling con-

ditions to physiological temperatures (18–30°C) (Paull and Rohrbach, 1985). The crown is also more susceptible to CI than the fruit itself (Paull and Rohrbach, 1985).

Partial control of CI symptom development has been achieved by waxing, polyethylene bagging (Paull and Rohrbach, 1982, 1985; Rohrbach and Paull, 1982; Abdullah *et al*., 1985), heat treatments (Akamine *et al*., 1975; Akamine, 1976), controlled atmospheres (Abdullah *et al*., 1985; Paull and Rohrbach, 1985), ascorbic acid (Sun, 1971) and application of the ethylene inhibitor 1-methylcyclopropene (Selvarajah *et al*., 2001).

Postharvest changes in fruit quality

Both postharvest storage and waxing of pineapple at low temperature (8°C) can alter external and internal fruit characteristics (Chen and Paull, 1995). Shell yellowing increases slightly during storage at 8°C, while there is little change in overall shell appearance. The rate of skin yellowing upon removal of fruit from 8°C to 22°C and of fruit continuously held at 22°C is similar. Shell appearance declines quickly in fruit stored at 8°C and removed to 22°C, while fruit held at 22°C begin to lose appearance after 8 days at 22°C. Juice pH declines from 3.5 to 3.1 during 14 days' storage at 8°C, while TA increases. Juice pH of non-stored fruit and fruit removed from 14 days' storage at 8°C to 22°C declines in parallel to 3.3 from 3.5 in non-stored fruit and to 2.8 in stored fruit. Citric acid content increases slightly, with little change in malic acid during storage at 8°C. There was no change in malic or citric acids in fruit held at 22°C. The TA of non-stored fruit does not change for 8 days at 22°C and then increases *c*. 20% before declining. Fruit previously stored and then removed to 22°C show a continuous decline in TA from 135 1 to 85 mEq l^{-1}. Waxing fruit prevents the storage decline in juice pH at 8°C and reduces the increase in TA. Ascorbic acid initially increases and then decreases during storage at 8°C (Teisson and Martin-Prevel, 1979; Chen and Paull, 1995) and increases when held at 22°C. Storage for 2 weeks at 10°C has little effect on TSS or the content of individual sugars (Paull, 1993; Chen and Paull, 1995).

Changes in phenols, especially postharvest and during storage, has been associated with CI (Teisson, 1977; Paull and Rohrbach, 1985). Total phenols and PPO are low at harvest but increase dramatically following storage at 8°C in sensitive fruit (van Lelyveld and de Bruyn, 1977; Teisson and Martin-Prevel, 1979). The total phenol levels decline as chilling-induced browning develops (Teisson and Martin-Prevel, 1979) and increase in fruit stored at ambient temperatures postharvest (Paull, 1993), but changes in the levels of the individual phenols vary (Teisson and Martin-Prevel, 1979).

Postharvest insect disinfestation

Pineapple fruit (cv. 'Smooth Cayenne') irradiated with 300–500 Gy show delayed shell degreening with no effect on flavour, TSS or crown appearance (Upadhya and Brewbaker, 1966), while 'Queen' pineapple fruit showed browning of the skin and softening of flesh at doses greater than 250 Gy (Damayanti *et al*., 1992). Rooting of crowns treated with greater than 150 Gy is inhibited.

Postharvest physiological disorders

Chilling injury

Fruit CI has been called endogenous brown spot, physiological breakdown, black-heart and internal browning, with the latter being more common (Plate 38). The symptoms of CI include: (i) wilting, drying and discoloration of crown leaves; (ii) failure of green-shelled fruit to yellow; (iii) browning and dulling of yellow fruit; and (iv) internal flesh browning (Lim, 1985; Paull and Rohrbach, 1985). CI symptom development can be divided into two events: the first relates to the exposure to temperature less than 10–12°C (Fig. 10.7), while the second is tissue darkening, which can range from brown to black (Paull and Rohrbach, 1985). After exposure of fruit to 10–12°C, tissue darkening (Fig. 10.7) is more pronounced between 17.5°C and 27.5°C (Paull

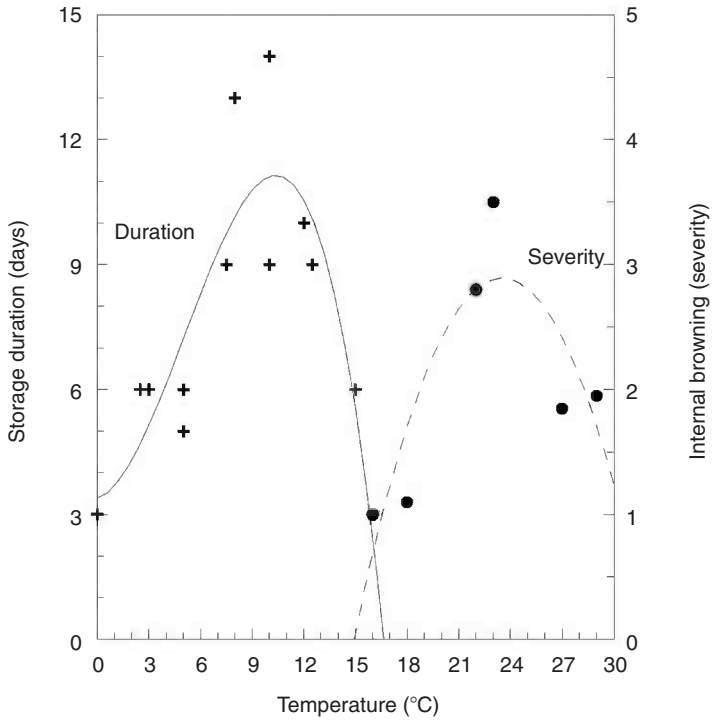

Fig. 10.7. Chilling-induced internal browning of pineapple stored at various temperatures for different length of storage and then removed to higher temperature, generally 20°C (data from Akamine, 1963; Smith, 1983; Paull and Rohrbach, 1985; Abdullah *et al*., 1986), and effect of different temperatures after removal from 14 days at 8°C on development of internal-browning severity (from Paull and Rohrbach, 1985).

and Rohrbach, 1985). The development of tissue darkening is also related to preharvest shading and low temperatures (Linford, 1932; Akamine *et al*., 1975; Keetch and Balldorf, 1979; Swete Kelly and Bagshaw, 1993), ascorbic acid content (Miller, 1951; Teisson and Martin-Prevel, 1979; Paull and Rohrbach, 1985; Abdullah *et al*., 1986), lower sugars and opaque fruit (Abdullah and Rohaya, 1983; Paull and Rohrbach, 1985), storage atmosphere (Paull and Rohrbach, 1982; Hassan *et al*., 1985) and clone (Wilson Wijeratram *et al*., 1993; Sanewski and Giles, 1997). The symptoms are seen occasionally in Hawaii's cool-season fruit (Akamine *et al*., 1975) and can be more severe on the northern side of a bed than on the southern side.

The occurrence of CI following exposure to temperatures between 12 and 21°C (Smith, 1983) is difficult to reconcile with published findings and may be related to preharvest stress (Swarts, 1991; Swete Kelly and Bragshaw, 1993) or a delay in symptom development at these temperatures. Partial to complete control of CI symptom development has been achieved by waxing, polyethylene bagging (Paull and Rohrbach, 1982, 1985; Rohrbach and Paull, 1982; Abdullah *et al*., 1985; Paull and Rohrbach, 1985), heat treatments (Akamine *et al*., 1975; Akamine, 1976), controlled atmospheres (Abdullah *et al*., 1985; Paull and Rohrbach, 1985) and ascorbic acid application (Sun, 1971). Selection of hybrids for higher flesh ascorbic acid concentration significantly reduces CI symptom development and presumably storage life.

Flesh translucency

Translucency is a physiological disorder where the pineapple fruit flesh shows water-

soaking symptoms. Translucency, as opposed to opaqueness, lacks the presence of small air bubbles in the intercellular spaces of the fruit flesh tissue and has a higher SG (Sideris and Krauss, 1933a). The SG can be employed as a non-destructive method for the detection of fruit translucency. Translucent fruit are extremely fragile, making these fruit very prone to mechanical injury during harvest, postharvest handling (Py *et al*., 1987) and shipping as fresh fruit. In addition, translucent fruit are more susceptible to diseases (Gortner *et al*., 1963) and preharvest sunburn (Keetch, 1977). Highly translucent fruit have flat and overripe off-flavours and a significantly lower edible quality (Bowden, 1967).

The incidence of peduncle leakage is correlated with translucency severity, and this leakage keeps the broken peduncle wet and may lead to unsightly, dark bluish grey *Penicillium* growth postharvest (Paull and Reyes, 1996). Translucency occurs before harvest (Bowden, 1969; Rohrbach and Paull, 1982; Paull and Reyes, 1996) and generally the basal flesh is the first to show symptoms; in severe cases the whole fruit is affected (Paull and Reyes, 1996). Translucent fruit are more common in the cooler season (Fig. 10.8). Waxing can reduce the rate of translucency development after harvest in low shell-colour fruit. Soler (1993, 1994a) regards translucency as being due to early flesh senescence; however, it is apparently also related to the weather 3 or more months before harvest (Paull and Reyes, 1996). Fruit with larger crowns have a lower incidence and severity of translucency.

Fruit with increasing translucency have increased pH, TSS/acid ratio and fruit weight and decreased total esters, and acids decline. The decline in organic acids during ripening is more pronounced in translucent (Sideris and Krauss, 1933a) than in opaque fruit, while sugars show little change. Translucent fruit usually have a higher TSS-to-TA ratio than opaque fruit, due to lower acidity (Sideris and Krauss, 1934; Bowden, 1969).

The cause or causes of translucency are unknown. Translucency in Hawaii has been associated with clones, high nitrogen, large vigorous plants, spring-ripened fruit, treatment with fruit-enlarging agents, irrigation rate, planting density, larger crowns and environmental factors (Paull and Reyes, 1996). Paull and Reyes (1996) found that both crown weight and fruit translucency at har-

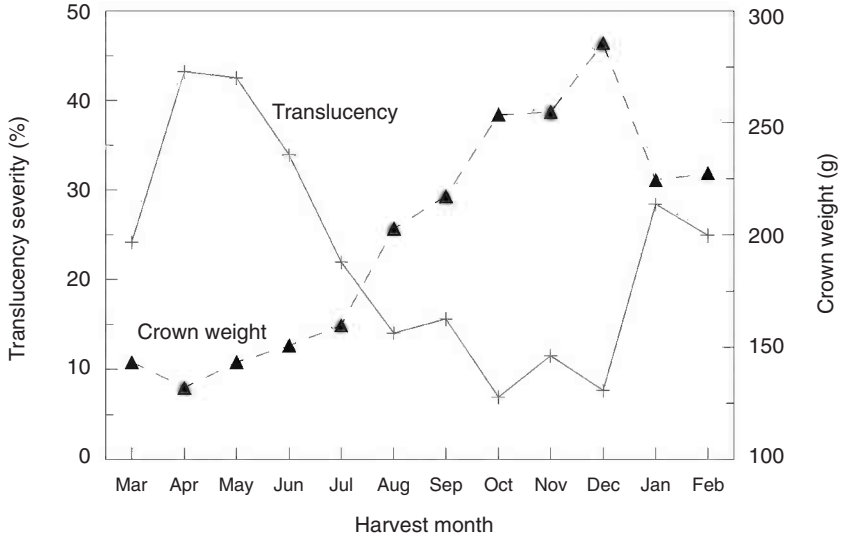

Fig. 10.8. Variation in crown weight and fruit-translucency severity at different times of the year (from Paull and Reyes, 1996).

vest are correlated to the monthly average air temperature 2–3 months before harvest, and the correlation between crown weight and translucency severity was significantly negative. However, removing the crown either at an early or at a late stage of pineapple fruit development did not have any significant effect on fruit weight or translucency (Chen, 1999). The significantly negative correlation between the air temperature 2–3 months before harvest and translucency (Paull and Reyes, 1996) is possibly related to an increase in heat tolerance of fruit flesh, due to their higher fruit temperature (Chen, 1999).

Pineapple fruit translucency has been suggested to be related to an increase in cell-wall hydrolases (Soler, 1993) and membrane permeability (Soler, 1994a). High calcium concentration may decrease the secretion or activities of cell-wall hydrolases (Huber, 1983) and membrane permeability; however, calcium concentration and the divalent cation-binding capacity of cell walls in pineapple fruit flesh decline with development (Chen, 1999). Pineapple fruit translucency increases with increasing fruit weight (Bowden, 1969), possibly due to a decrease in calcium concentration, since larger fruit may need more calcium to stabilize cell membranes. When fruit cannot acquire sufficient calcium, cell membranes may lose integrity and lead to leakage and translucency.

Basal fruitlets show translucency first. These tissues have higher sugar content than the interfruitlet tissue and the flesh at the top of the fruit, respectively, suggesting that translucency is related to maturity. Chen (1999) reported that plant defoliation conducted 3 or 4 weeks before harvest decreased the pineapple fruit flesh TSS and translucency. There was a linear cause–effect relationship between percentage of defoliation and TSS and translucency. Defoliation did not significantly affect the membrane permeability of pineapple fruit-flesh cells, suggesting that translucency caused by sugar unloading is different from translucency caused by heat stress, and the former was much more significant at the later stages of fruit development.

The intercellular spaces are filled with liquid in translucent pineapple fruit-flesh tissues, suggesting that a higher osmotic pressure exists in the apoplast than in the symplast, which steepens the pressure gradient between the phloem end and the flesh cells, where unloading is occurring. The higher apoplastic osmotic pressure and water uptake due to increased sugar storage in the apoplast could favour the occurrence of pineapple fruit translucency. CWI activity in pineapple fruit flesh increases rapidly 4 weeks before harvest and is followed almost immediately by the first symptom of translucency. A positive correlation also exists between the CWI activity and the severity of translucency (Chen, 1999). The CWI activities in the tissues that first show translucency – the basal fruitlet and basal flesh – are significantly higher than in the interfruitlet tissue and the fruitlets and associated flesh of the top of the fruit, respectively. This suggests that CWI in the pineapple fruit flesh could be a positive factor in the occurrence of translucency.

Translucency can occur when the fruit shell is still green (Py *et al.*, 1987). The green-shell translucency is found more frequently during high-temperature periods (Green, 1963) and may be due to lesions in the cell membrane caused by either high temperatures or too abundant supplies of sap brought about by a sudden improvement in the water-supply during a period of intense photosynthetic activity, or both (Py *et al.*, 1987). Soler (1993, 1994b) showed that green-shell translucency, at a biochemical level, is characterized by an increase in catalase, α- and β-galactosidase activities and ascorbic acid synthesis, which might be related to translucency by the modification of membrane galactolipids and permeability changes. Pineapple fruit flesh became susceptible to high fruit temperature-induced leakage and translucency at the later stages of fruit development (Chen, 1999). Sideris *et al.* (1935) suggested that flesh translucency and shell degreening were independent phenomena associated with fruit senescence, with the flesh of green ripe fruit senescing before shell degreening started. These green-shell translucent fruit degreen rapidly when treated with ethephon.

Pineapple fruit translucency, which normally occurs at the later stages of fruit development, is therefore due to a combination of effects, related to both high fruit temperature and fruit maturity. Associated factors affecting the severity of translucency include a decrease in calcium concentration of fruit flesh and of divalent cation fruit-flesh cell-wall-binding ability, which leads to a loss of cell-membrane integrity and cell-wall rigidity. These changes are followed by an increase in membrane permeability and an enhanced susceptibility of fruit flesh to high temperature. Increased sucrose accumulation and the activity of CWI favouring apoplastic phloem unloading cause an increase in the solute concentration and liquid volume in the apoplast, which in turn leads to translucency.

Crown dehydration

The crown is a continuation of the vegetative stem leaves, and the spirally arranged leaflets have a similar morphology. The stomata are located in furrows on the underside of the leaf, which is also covered by trichomes. The stomata in mature leaves open at night and are closed during the day, associated with crassulacean acid metabolism (Sideris *et al*., 1948). However, the stomata of young leaves such as on the crown, may not show this same diurnal function (R.E. Paull, 1985, unpublished results), as water-loss rate appears to be constant during storage. At 10°C, stomatal opening and closing are slowed and CO_2 uptake is reduced, compared with 17°C (Kent, 1967). Ethylene increases leaf respiration, causes stomatal opening and enhances dehydration (Dull and Staruszkiewicz, 1966). Opening of stomata requires illumination on the preceding day and ethylene negates this requirement (Kent, 1967). Hence, what has been reported for plant leaves may also occur with the crown leaves, such as sensitivity to low temperatures and ethylene response.

The crowns of fresh fruit soon lose their green healthy look and the leaves become dehydrated and necrotic. The oldest leaves are generally most affected, and this is possibly due to ethylene. Postharvest ethylene treatment leads to greater water loss than if crowns are untreated. Rate of dehydration is also related to the relative humidity of storage (Dull and Staruszkiewicz, 1966). A well-ventilated crown can lose up to 10% of its weight in 14 days, while a crown treated with 200 µl l^{-1} ethylene can lose up to 64% of its fresh weight. Waxing of the crown frequently leads to phytotoxicity and excessive water loss, and some paraffin-wax formulations can slightly reduce weight loss (Schappelle, 1941).

Sunburn

Sunburn is common during hotter periods (> 35°C) (Keetch and Balldorf, 1979), when the fruit is not shaded by leaves, and especially in ratoon crops. Fruit flesh temperatures on the exposed side of the fruit in the field can be 15°C higher than the air temperature of about 27°C, and the crown leaves provide little protection. The condition is more prevalent in the outer rows of a field and when there is reclining fruit. Drought in the warm season can lead to weak peduncles and lodging of fruit, while fruit that develop in the cool season also tend to have longer peduncles, which are inclined to tip over. Forcing immature plants to flower also leads to longer peduncles, which have a greater tendency to lodge (Dalldorf, 1979). Sunscorched fruit first show a bleached yellow-white skin, which turns pale grey and brown (Plate 40), with damage to the flesh underneath, which softens and may extend to the core (Linford and Spiegelberg, 1933). Cracking of the shell and flesh can occur. These damaged areas are more susceptible to disease organisms (Lim, 1985). If the sunburn occurs early in growth, it can lead to irregular fruit shape and an off-centre core.

Malformations

Knobs on the base of fruit, a mutation (Collins, 1960), occur in off-types. Culling of these fruit crowns reduces the subsequent field incidence. These fruit are not marketed, as trimming allows rots to develop where the knobs are removed. The other genetic

off-type is multiple crowns (fasciation), two or more on each fruit, with the fruit taking on a flattened appearance. This condition is linked to high temperatures at flower induction (Soler, 1992b) or too succulent vegetative growth prior to forcing. These fruit may not be marketable and it has been recommended that the crowns should not be used for planting, even though the condition is not inherited (Linford and Spiegelberg, 1933). Fruit with pronounced 'eyes' or fruitlets are normally not accepted in fancy grades of fruit and the thicker skin means lower flesh recovery. This condition is common in fruit that have flowered during cool weather.

Broken and hollow core

A transverse break in fruit flesh that occurs early in development is marked by a slight depression on the outside of the fruit (Lim, 1985). The break leaves a gap of 2–10 mm in the flesh and the tissue becomes corked and brown, sometimes accompanied by rot. The upper portion of the fruit usually ripens before the lower half. This condition is not seen in 'Smooth Cayenne', but is common in 'Singapore Spanish'. Hollow core refers to a vertical crack in the core that becomes dry and leathery and it may extend to the peduncle (Plate 41). The fruit are usually opaque and the condition is thought to be due to desiccation.

Seediness

Seediness can sometimes be a problem, as the seeds are brown and hard. This occurs with 'Smooth Cayenne' selections and where different clones are planted in close proximity.

Mechanical injury other than due to handling

Rodents (Plate 42), birds, insects (crickets, grasshoppers, etc.) and wind may cause wounding in young fruit that will heal over with hard, corky, scar tissue. Fruit growth may tear open this injury and lead to misshaped fruit.

Deep eye

One or more of the seed cavities of a fruitlet turns firm and brown and the tissue becomes leathery or corky. These lesions can be elongated, triangular or rounded (Linford and Spiegelberg, 1933) in cross-section. They are more prevalent at higher than at lower elevations and are induced by a number of causes, including: natural opening into the cavity, failure of the carpels to close during development, chemical burns or insects. Some clones are highly susceptible to this condition.

Shell surface pitting

There is shallow brown pitting of sepals and bracts that does not extend more than 6 mm into the fruit, and the affected tissue shrinks. This condition is most often found in opaque fruit with yellow shells in fields where a heavy dew or light shower frequently moistens the fruit (Linford and Spiegelberg, 1933).

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11 Processing

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Processing Operations

Harvesting

The quality of any processed food begins with the ingredients used. In the case of processed pineapple, the fruit should be harvested at the optimum stage of maturity to obtain high quality products. Since the pineapple does not ripen once it is harvested from the field, the fruit should be sufficiently ripened in the field to endow the flesh with high pigmentation and full pineapple flavour, but not so ripe that the fruit cannot be successfully transported and handled through the processing system. Pigmentation can be measured as concentration of carotenoids and similar pigments that can be extracted and measured at predetermined wavelengths. These pigment values tend to be positively correlated with favourable flavour components and are good indicators of ripeness.

Fruit is usually selected by shell colour. To maximize solid-pack recovery and yield, fruit of various shell colours are sampled prior to harvesting and are processed through a special line in the cannery. Based on the results, a harvesting shell-colour range is recommended and pineapples of the recommended shell-colour range are then harvested by hand and often loaded with the aid of a mechanical harvester.

Different shell colours may be assigned to large and small fruit in the same field, with the smaller fruit usually being picked at the higher shell colours. A seven-point scale may be used where 0 denotes a full-green or underripe pineapple and 7 denotes an overripe pineapple. Since shell colour is not an absolute indicator of fruit ripeness, fruit sweetness as °Brix, measured with a calibrated refractometer, is also taken.

Particular care should be taken in the use of fruit-ripening hormones, e.g. ethephon, as these materials may change the external appearance of the fruit by removal of chlorophyll, without an equivalent increase in the fruit Brix or the flavour profile of the fruit. Improvements in fruit quality can result from hormone treatment if the fruit has already started the maturation process, showing both internal translucency and colour development with at least measurable soluble solids of 12°Brix at the time of treatment.

Fruit crowns may be removed mechanically or manually after harvesting, either in the field or at the cannery. The usual practice is to remove the crowns from cannery fruit in the field. Crowns, however, may be transported with the fruit to the cannery to serve as cushions to minimize fruit bruising and to bring the fruit crowns to a central location for size grading and treatment. These fruit crowns may be used as planting materials for the next planting. Because all pineapples in a field do not ripen at the same time, each

*Retired.

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field may have to be harvested several times to obtain optimum quality and yield.

Pineapples are immediately transported to the cannery in large bins in such a manner as to minimize fruit bruising and maintain fruit quality. Gentle and expedient handling of the fruit is required to reduce quality and recovery losses, with all received fruit generally being processed within 24 h of harvest.

Fruit bruising and fruit spoilage, as a result of rough handling, uneven road surfaces or delayed transport, can lead to poor quality and significantly reduce cannery recovery of prime products. In addition to the use of crowns mentioned above, care should be given to all aspects of handling and fruit movement. All hard or sharp contact surfaces should be either eliminated or padded to protect the fruit. The depth to which fruit are loaded is usually limited. In some cases pineapples are carefully stacked end to end to minimize side bruising. Field roads should be maintained in a well-graded condition and the transportation trucks may be equipped with air-ride suspension or the equivalent to minimize transportation damage.

Fruit receiving

To reduce losses in quality and recovery, all received fruit should be processed within 24 h of harvest. Trucks with bins containing up to 6 tons of decrowned fruit are weighed on a scale at the cannery upon arrival. Details regarding the origin of the fruit are carefully recorded. Such record-keeping practices are becoming increasingly important in developing trace-back information, which can be used in the event of product recall or any other activity that may require limiting the scope of investigation related to finished products. The type of information being gathered will vary among fruit obtained from private growers, cooperatives, or contract growers or from fields owned and/or operated by the cannery.

Before the fruit are unloaded, samples may be taken from the arriving load to assess fruit quality, size distribution, shell colour, disease incidence, possible pest infestation or flesh nitrate level. These indices can affect how and when the fruit will be processed. Fruit are then carefully unloaded and stacked near the fruit-dumping station for immediate processing.

Unloading may be accomplished by hand, by dumping into water or by hydraulic lifts, which raise the bins and gently unload the fruit on to conveyors that lead to the size graders. Careful fruit unloading is another critical factor in minimizing fruit bruising (Timm and Brown, 1991). Water has been shown to be one of the best methods of unloading, where fruit drops directly into a flume of water that is deep enough for the fruit to be moved away from other unloaded fruit and others that have sunk before being elevated out of the water to the size graders. Salt water has been effectively used to separate translucent fruit from opaque fruit, which may be unacceptable in some fresh-fruit markets.

Grading for fruit size is one of the most important activities in maximizing the recovery of marketable products. A precise determination of the relationship between fruit diameter and recovery should be made for each growing area and each clone of pineapples being grown. Seasonal variations in recovery should also be checked to ensure that there are no major differences. The normal procedure used in determining the ideal grader settings is to separate fruit by small increments of diameter, e.g. $1/16$ in. or 1.5 mm, and to evaluate all fruit in a diameter class for product recovery. If slice products are of the highest value, then this measure may be sufficient as a means of determining optimum recovery. Others may choose to assign values to all products and determine the optimum economic recovery.

Table 11.1 demonstrates the relationship between individual fruit weight and cylinder weight. The points at which the recovery curves for each Ginaca knife size intersect determine the critical settings for the graders. All grader performances should be checked, using precisely machined, hand-held graders. These consist of two parallel bars, separated at predetermined distances to measure fruit diameters (Fig. 11.1).

Once the fruit are properly graded, size distribution to the Ginacas should be con-

Table 11.1. Relationship between individual fruit weight and cylinder weight.

1T weight (kg)		2T weight (kg)		$2\frac{1}{2}$ weight (kg)	
Fruit	Cylinder	Fruit	Cylinder	Fruit	Cylinder
0.73	0.19	1.23	0.40	1.83	0.64
0.74	0.23	1.25	0.39	1.86	0.61
0.75	0.20	1.26	0.41	1.88	0.64
0.75	0.21	1.28	0.41	1.90	0.63
0.75	0.23	1.30	0.41	1.90	0.71
0.76	0.21	1.32	0.42	1.94	0.66
0.76	0.25	1.32	0.41	1.94	0.69
0.79	0.23	1.33	0.41	1.95	0.68
0.79	0.23	1.35	0.41	1.96	0.67
0.81	0.22	1.35	0.44	2.02	0.66
0.81	0.24	1.36	0.44	2.02	0.68
0.82	0.22	1.37	0.45	2.01	0.71
0.83	0.24	1.42	0.44	2.01	0.70
0.84	0.23	1.42	0.46	2.08	0.72
0.84	0.25	1.44	0.47	2.10	0.68
0.91	0.26	1.47	0.47	2.10	0.69
0.91	0.31	1.50	0.47	2.13	0.73
0.94	0.24	1.51	0.46	2.15	0.69
		1.51	0.47	2.18	0.75

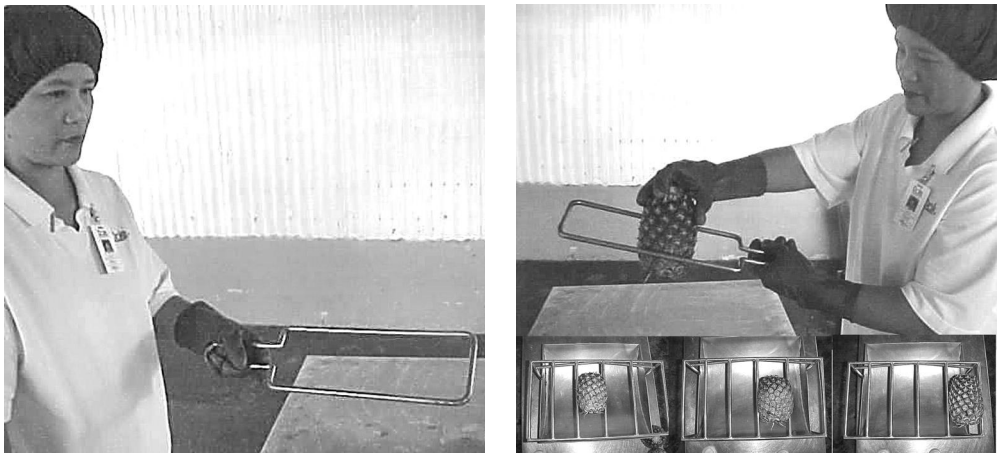

Fig. 11.1. Hand-held pineapple grader.

trolled to keep the cannery in balance between the various fruit sizes with a minimum number of changes to the Ginaca settings. This can be accomplished by the use of accumulators for each major fruit size and unloading fruit that complement the desired size requirements, based on information gathered at fruit receiving.

Fruit may be divided into size classes by counter-rotating screws, which use fruit diameter to grade fruit into processing size classes (Table 11.2). The smallest fruit that falls through the grader rolls at the narrowest part is classed as Sub 1T (Cruess, 1938). The other fruit sizes in increasing diameter are 1T, 2T and $2\frac{1}{2}$. These designations are

Table 11.2. Fruit diameter for grading.

Size class	Fruit diameter (cm)
Sub 1T	< 9.21
Small (1T)	9.21–10.80
Medium (2T)	10.80–13.02
Large ($2\frac{1}{2}$T)	>13.02

derived from equivalent can sizes in which slices cut from these fruit would fit conveniently. The Sub 1T fruit is frequently used for juice. The graded pineapples then fall into three separate conveyors of parallel water flumes, one flume per fruit diameter, each flume also serving to partially wash the fruit. Since overripe pineapples sink because their density values are greater than that of water, a water flume may be used to separate and wash them. At the end of the flumes, graded and washed pineapples are lifted by conveyors and sprayed with a chlorinated water rinse at approximately 20 p.p.m. chlorine. The graded and rinsed fruit are then transferred to other conveyor belts headed to the fruit preparation areas.

Fruit preparation

Distribution conveyors receive and feed the graded and rinsed fruit to chutes located immediately before the Ginaca machines. An operator regulates the feeding of pineapples to the Ginaca machines and manually removes cracked, smashed, fermented and other unsound fruit. Each Ginaca can be set up to process a specific diameter class of fruit by having it fitted with an appropriate diameter-sizing knife. Some Ginaca machines can be modified to handle other diameter classes. The Ginaca machine centres each fruit over the sizing knife, which splits the shell, allowing a cylinder to pass through the circular knife. A rotating drum takes the shell away, which then passes over a set of eradicator blades, which strip off the juice material (also called 'juice blanket') from the shell material. The fruit cylinder passes into one of a series of turrets, which enables each end of the cylinder to be removed at a predetermined depth. Additional juice material may be recovered from these end cuts. While the cylinder is in the turret, the core is also removed and is added to the juice-material stream. The cylinders are further prepared to produce high-value products, such as slices, chunks, titbits and crush. The peel, crown-end and bottom-end materials are all used for production of by-products. Typical Ginaca speeds vary according to fruit size, with 56 large-sized, 85 medium-sized and 96 small-sized fruit per minute (Lingle, 1986).

Trimming

The resulting pineapple cylinders then proceed to trimming tables, which are set up as either slice tables (for slices, titbits, crushed and juice) or chunk tables (for chunks, crushed and juice). Inspectors at the trimming tables manually remove blemishes and any adhering shell. Trimmed cylinders are then conveyed to the slicer. Edible trimmings are placed on conveyor belts headed for the juice preparation area, whereas inedible portions (all materials with skin or blemish) are separated and pass on to the by-products manufacturing area.

Slicing

Slicers are equipped with single or multiple-gang slicer blades, which are set to cut slices for slice packs. Slices are used to produce titbits, cubes and chips. Thicker slices are cut for the production of chunks or pieces. Almost all materials can be used to manufacture crushed pineapple. Material with a high amount of core, such as core chips from recoring, should be avoided because, depending on specific product specifications, there is a limit to the amount of core material allowed in crushed pineapple.

Packing

A maximum pH of 4.6 is required if packed as a high-acid product. If necessary, citric acid can be added if there are individual cylinders that have low natural levels of acid.

Solid packs

A wide variety of styles of product may be packed from pineapple. The standard ones are listed in the excerpt from the Codex standards for canned pineapple (Codex Alimentarius Commission, 1995). These standards further describe types of packs, packing media, composition and quality criteria, including defects and their tolerances. Minimum requirements are also outlined for weights and measures and labelling of products entering international trade.

More specific standards may be outlined in national or other standards used to define expectations of specific packs. For example, the Campden Food and Drink Research Association has provided standards for canned pineapples, which can be used as criteria for packing and evaluating canned pineapple products (Campden Food and Drink Research Association, 1991a,b). Similarly, the US Department of Agriculture has published *Standards for Grades of Canned Pineapple* (USDA – Agricultural Marketing Service, 1990).

Details of the various standards are not listed here, but they should be used as references when setting standards for packing products of various styles to meet specific market requirements.

CYLINDER PACKS. Following the preparation of the cleaned fruit cylinders, whole cylinders to be used in cylinder packs are cut to a specified length to fit the cans in which they are to be packed. Whole cylinders may also be recut radially into spears or fingers of a length to fit the specified can size.

SLICES. Slices are graded by packers as fancy (geometrically perfect, excellent and uniform colour and whole), choice (not as perfect and with less colour) or standard, each grade to meet specifications. Slices are packed manually or automatically into cans. Slices may be further cut as titbits or cubes. For a graphic description of the cutting process, see Rohrbach and Johnson, Chapter 9 this volume.

Slice defects due to Ginaca malfunction include:

1. Off-centre: when the core hole is not centred in the slice to prescribed limits.
2. Off-centre core: when the core is not in the centre and the core hole is.
3. Off-core: when the core is in the centre and the core hole is not.
4. Large-core: when core tissues remain around the core hole

Since slice defects due to Ginaca malfunction affect maximum recovery of premium pineapple products, it is important to monitor and minimize slice defects.

Other slice defects are due to:

1. The presence of too much core tissue.
2. Coarse texture from the upper portion of the cylinder and lighter colour from less mature fruit.
3. Physical damage, such as breaking, bruising or splitting.
4. Blemishes in excess of $1/16$ in.
5. Gouges from removal of blemishes.

CHUNKS AND TITBITS. Chunks come from thicker slices, the dimensions of which will vary with the diameter of slices used. Chunks and titbits from slices of significantly different diameter, e.g. 1T and $2\frac{1}{2}$ should not be mixed. If chunks or titbits are being produced, inspected slices may either proceed to the end of the table, where they are cut, or be placed in pans and taken to another location for cutting. Broken pieces and rejected slices pass over the end of the table (thereby, called table-end material) and are used in juice or crushed-pineapple preparation.

Once packed, the cans are filled with packing medium. This may follow treatment in an exhaust box, in which the product is heated and subjected to vacuum to remove entrapped air from the tissues. Packing medium is usually heated to above 60°C to prevent any microbial growth in the medium during its use.

The product is hermetically sealed under vacuum and then transferred to a cooker, where it is subjected to enough heat for a sufficient period of time to ensure that all organisms that could cause spoilage are killed.

CRUSHED PINEAPPLE OR CRUSH. All table-end materials are gathered and conveyed to an inspection table, where all extraneous and off-quality material is removed. High-quality crushed pineapple should show discrete particles with no core or discoloured pieces due to the presence of skin or blemishes. Crushed pineapple may be designated for the retail or the institutional markets. Crushed products for the institutional market in the USA require a much heavier drained weight, which is achieved by heating before filling so that excess juice released in the cooking process may be drained away. As the cooking temperature is increased, more juice is released. There are two types of crushed-pineapple products for the institutional US market: coarse-cut and fine-cut, with the latter type requiring a heavier drained weight. After the proper drained weight is achieved, the product is heated to filling temperatures and hot-filled in no. 10 cans. Multiple rotary coolers are used to cool crush to 54°C.

After appropriate draining, crushed pineapple for the retail market is hot-filled at 86–90°C with a volumetric filler, inverted in the container, held for several minutes, depending on the size of the container, and cooled in rotary coolers to at least below 54°C.

Juice

Both solid and liquid fruit components from all Ginaca machines and trim tables are used in pineapple-juice production. Solid components consist of the following materials:

1. Pineapple cores: fruit centres removed by the Ginaca machines during peeling operations.
2. Eradicator meat: the thin layer of flesh between the shell and the fruit cylinder removed by the Ginaca machines.
3. Trimmings: end cuts from the Ginaca machines and fruit pieces from the trimming and preparation tables.
4. Whole fruit: the Sub 1T and other fruit sizes not required for solid packs or crushed.

The use of any other solid pineapple materials for juice production is not allowed for products sold in the USA. Any objectionable material is removed from the solid pieces over an inspection belt. These raw materials are then conveyed over screens that drain the free-juice component. Clean solid particles then pass through a disintegrator, which breaks down the pulp for easier juice extraction. A multiple-stage screw press is then used to extract pineapple juice from the solid constituents, maximizing recovery to about 90%. Juices from liquid components, consisting of all surplus juice obtained during any processing activity, and juice from the solid-fruit components are then blended with agitation in large tanks. When juice foaming occurs due to the presence of gums, up to 10 p.p.m. of food-grade antifoam may be added to reduce foaming. The juice is then heated in tube or plate heat exchangers to about 60°C and passed to continuous, automatic, desludging-type centrifuges to eliminate insect fragments, shell pieces and excess pulp. The insoluble-solids content of pineapple juice, which is important to the perceived mouth-feel of the product, is controlled by centrifugation in the range of 5–30%. Centrifuged juice is then stored in a tank equipped with an agitator and may be processed to produce single-strength pineapple juice, blended with other fruit juices or concentrates to produce juice blends used as packing medium, or evaporated to produce pineapple-juice concentrate.

Single-strength juice may be packed through a hot-fill process, cold-fill process or aseptic process. The hot-fill process involves filling the cans with juice preheated to about 96°C, seaming the can lids, inverting the cans, holding at this temperature from 1 to 3 min depending on the can size, and cooling to about 38°C. The cold-fill process involves filling the cans with juice at about 60ºC, seaming the can lids, processing in continuous, agitating cookers to product temperatures greater than 87.7°C and cooling in continuous, agitating coolers to about 38°C. The aseptic process entails sterilizing the product and package separately, usually with the use of high-temperature, short-time heating and filling the sterile containers with sterile product under sterile conditions.

Pineapple-juice concentrate may be prepared using low-temperature, multiple-effect

(stages), tube or plate evaporators. Pineapple essence, usually obtained from the first effects, is added back to the final concentrate to enhance the flavour. Pineapple-juice concentrates, commonly sold as $4\frac{1}{2}$:1, 61°Brix, 3:1, 46.5°Brix, or 6:1, 72°Brix concentrates, are packaged in both aseptic and frozen forms. For a detailed description of pineapple-juice processing, please refer to Hodgson and Hodgson (1993).

Other products

PINEAPPLE BRAN. Since approximately 35–40% of the fruit weight is in the skin and ends, proper solid-waste disposal becomes a serious consideration in pineapple-processing operations. The simplest solution that is currently followed by many processors is to return it to fields and use it as a soil amendment. Because of its high moisture content, it easily ferments and presents storage problems. To reduce this moisture content, other operations macerate the skin and ends to produce a coarse pulp and press out the liquid it contains – mill juice. The resulting solid material, called wet pineapple bran, is suitable for cattle feed. If dried to a moisture level of less than 12%, the product is known as pineapple bran, which can be easily stored.

MILL JUICE. This is the liquid pressed from macerated pineapple skins during pineapple-bran production. Although it has a lower soluble-solids content and higher acidity than pineapple juice, mill juice has approximately the same composition but contains some undesirable flavour materials and heat-darkening agents, due to the Maillard reaction. Although an ion-exchange process is able to lower mill-juice acidity, an acid-modified pineapple juice cannot be designated as fruit juice by current US standards. Juice from other off-grade sources (e.g. rotten and damaged fruit) may be added to mill juice, concentrated and then added to wet pineapple bran to increase bran yield or may be used as a source of sugar in the production of alcohol and vinegar. When prepared under the same sanitary conditions as pineapple juice and if treated further to remove the off-flavour and off-colour components, mill juice has been successfully used as a sweetener in packing medium.

DIETARY FIBRE. Processed pineapple peels with 85% total fibre content and 1.0 kJ g^{-1}, as prepared by the Institute de Investigaciones para la Industria Alimentaria, Havana, Cuba, were used as a source of dietary fibre at 8% maximum moisture in a dried beverage mix (Larrauri *et al.*, 1994, 1995). A mild laxative effect is observed. Fibre from cores has been evaluated as a food-grade filler for some food products.

CANDIED PINEAPPLE. Candied pineapple is probably one of the most popular dried-pineapple products. This product is generally prepared using pineapple chunks or thick pineapple slices segmented with a knife. The chunks are soaked for 5 h in sugar syrup (about 60°Brix) containing an antioxidant, such as ascorbic acid or a sulphiting agent, to maintain colour and are then air-dried (Fig. 11.2). The dried pieces are sometimes coated with another layer of syrup and dried again.

Candied pineapple segments, which had been blanched and vacuum-treated to reduce colour oxidation, appeared turgid and translucent, with no signs of significant cytorrhysis but with severe plasmolysis. Its intracellular spaces were filled with liquid. Untreated candied samples appeared highly shrunken and opaque, with severe cytorrhysis and plasmolysis, and its intercellular spaces were filled with air (Chen, 1995).

ULTRA-HIGH-PRESSURE PASTEURIZED FRESH CUT PINEAPPLE. As a means of extending the shelf-life, fresh-cut pineapple chunks obtained from a commercial processor were packed in heat-sealed polyethylene pouches and treated under various ultra-high pressure (200, 270 and 340 MPa), temperature (approximately 4, 21 and 38°C), and time (5, 15, 40 and 60 min) combinations (Aleman *et al.*, 1994). Bacterial survival and total yeast and fungi counts generally decreased with an increase in processing pressure.

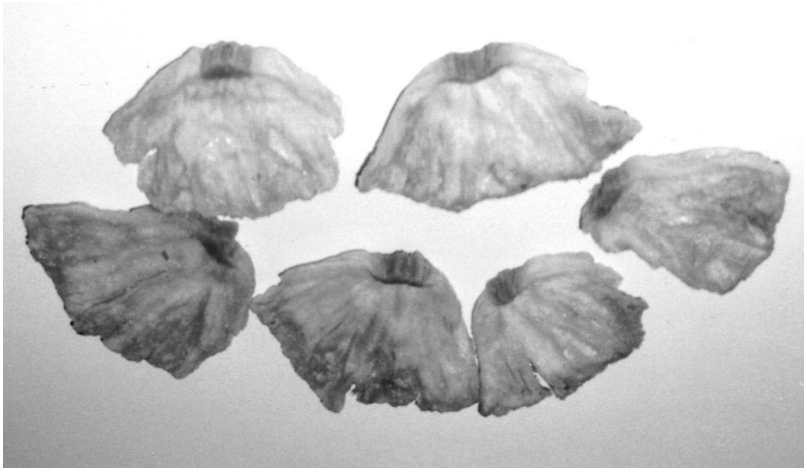

Fig. 11.2. Dehydrated pineapple chunks.

Quality assurance

All aspects of pineapple preparation, packing and processing should be carried out under conditions that meet the requirements of current good manufacturing practice, as outlined in 21 CFR 110 (FDA, 2001a). Starting on 22 January 2002, juice processors and importers are required by 21 CFR 120 to document a hazard analysis critical control point (HACCP) plan for each juice and juice product (fruit and vegetable juices, purées or concentrates) sold in the USA (FDA, 2001b). An HACCP plan documents that no hazards are reasonably likely to occur that could compromise the finished product. The regulations will bind small businesses starting on 21 January 2003 and very small businesses on 20 January 2004. For the definitions of small and very small businesses, consult 21 CFR 120.

Since many different pineapple products may be packed using different packing media, product cuts and various other styles, product coding accuracy is extremely important for proper product identification and tracing. It is equally important that product specifications be regularly monitored and that records accurately reflect operating conditions. Record-keeping remains one of the most important functions in quality control/quality assurance. It is recommended that the following checks of minimum standards be recorded:

1. Harvesting:
(*a*) Origin of the fruit.
(*b*) Date of harvest.
(*c*) Other fruit conditions, such as translucency or the occurrence of fruit diseases requiring specific handling.
(*d*) Shell colour.

2. Fruit receiving:
(*a*) Date of processing.
(*b*) Shell colour.
(*c*) Fruit quality.
(*d*) Size distribution.
(*e*) Disease incidence.
(*f*) Pest infestation.
(*g*) Flesh nitrate level.
(*h*) Other inspection comments.

3. Fruit preparation
(*a*) Clone of pineapple.
(*b*) Growing area.
(*c*) Seasonal variations.
(*d*) Amount of undersized fruit.
(*e*) Amount of oversized fruit.
(*f*) Degree of skin eradication.

4. Packing:
It is recommended that fruit be cooked within an hour of being placed in a container to prevent incipient spoilage.
(*a*) Solid packs:

(i) Colour and appearance before processing.
(ii) Colour and appearance after processing.
(iii) Frequency of occurrence of slice defects:

- Off-centre.
- Off-centre core.
- Off-core.
- Large-core.
- Presence of core tissue.
- Presence of less mature slices (coarse texture, lighter colour).
- Presence of physically damaged slices.
- Amount of discrete particles with core or discolored pieces due to skin and blemishes in crush.
- Amount of usable slices going to the crush line.

(iv) Drained weight:

- Crushed pineapple: drained weights of hot and cold pineapple to establish any correlated influences to fruit condition and dicer sharpness.

(v) Net weight.
(vi) Flavour; presence of off-flavours.
(vii) Aroma; presence of off-odours.
(viii) Any comments observed and corrective actions taken.

(*b*) Juice:
(i) °Brix.
(ii) % total acidity as citric acid.
(iii) Brix/acid ratio.
(iv) % insoluble solids.
(v) Container fill.
(vi) Visible defects.
(vii) Mould count using the Howard mould count method.
(viii) Vitamin C content.
(ix) % antifoam.
(x) % added sweetener.
(xi) Flavour; presence of off-flavours.
(xii) Aroma: presence of off-odours.
(xiii) Any comments made and corrective actions taken.
(xiv) At fewer frequency intervals, the following characteristics might be determined:

- pH.
- Processing temperatures: during filling, cooking and cooling.
- Packaging: vacuum, head-space, can-seam dimensions, physical damage, labelling defects, packaging defects.

Test methods and procedures are described in the US Food and Drug Administration *Standards of Identity, Quality, and Fill*; the US Department of Agriculture *Standards for Grades*; the Food and Agriculture Organization/World Health Organization (FAO/WHO) *Codex Standards*; the Association of Official Analytical Chemists *Official Methods*, and Volumes 1 and 2 of the National Canners Association *Laboratory Manual for Food Canners and Processors*.

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