TROPICAL FRUIT CROPS AND THE DISEASES THAT AFFECT THEIR PRODUCTION

R.C. Ploetz
Department of Plant Pathology, University of Florida, Homestead, FL USA

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Contents

Summary

Tropical fruits are important components of natural ecosystems. A limited number of the thousands of species that exist are important to humans, and only 50 or so are significant commercial products. Diseases affect all of these crops. The pathogens are all in the Eubacteria or Eukaryota. The Eubacteria include single-celled pathogens without cell walls (the Mollicutes), or with Gram-positive (the Firmicutes) or Gram-negative cell walls (the Proteobacteria). Important Mollicute pathogens of tropical fruit include the phytoplasmas, and of the Proteobacteria include species of *Erwinia*, *Pseudomonas*, *Ralstonia*, *Xanthomonas* and *Xylella*. Multicellular pathogens in the Eukaryota are most important, and include the predominant fungi; species in the Ascomycota (*Botryosphaeria*, *Ceratocystis*, *Fusarium*, *Glomerella* and *Mycosphaerella* are common genera) and Basidiomycota (e.g. *Armillaria*, *Erythricium*, *Ganoderma* and *Rigidioporus*) (together they comprise the Subkingdom Dikarya) are more numerous and important than all other groups of pathogens combined. Other eukarotic pathogens include the fungus-like oomycetes (e.g. *Phytophthora* and *Pythium* spp.), nematodes (*Meloidogyne*, *Pratylenchus*, *Radopholus*, and *Rotylenchus* spp. are most important), parasitic plants (especially the green alga, *Cephalueros*) and protozoa (*Phytomonas*). Nucleic acid-based pathogens, the viruses (single- or double-stranded RNAs or DNAs encased in protein or lipoprotein envelopes) and viroids (nonenveloped molecules of a few hundred nucleotides) are also important, but have unclear affinities to the above life forms. Among the most damaging are *Banana bunchy top virus*, *Citrus triztesa virus*, *Papaya ringspot virus* and *Coconut cadang-cadang viroid*. The epidemiology of these diseases influences what strategies are used in their management. When they are

available, disease-resistant host genotypes are often efficacious and cost-effective. These diseases are also managed with disease avoidance, exclusion, eradication and protection. Integrated combinations of these strategies are often needed to effectively manage these problems.

1. Introduction

Thousands of fruit species exist in the tropics, most of which are important components of tropical ecosystems. Some, such as figs, are keystones that influence community structure, the composition and abundance of associated taxa, and the survival and reproduction of community species. Many tropical fruit species are significant food and habitat resources. Complex and interdependent webs of fauna and flora are common in tropical systems, and species of plants that produce fruit play prominent roles.

Considered in this chapter is a small subset of this important group of plants, those that produce fruit whose pulp, mesocarp or juice are consumed by humans. Only about 300 of these fruits are considered major, and 50 are well known and important commercially. All of these crops are Angiosperms, and with the exceptions of members of the Magnoliid complex (i.e., annonas and avocado) and a handful of Monocots (banana, coconut, date, peach palm and pineapple), the important species are all Eudicots (tricolpates) (Table 1). Some of these plants, such as coconut and cashew, produce edible fruits but are also significant sources of other products (respectively, oil and fiber, and nuts). And other tropical plants that produce fruits are not considered here since their pulp or mesocarp are not significant; for example, only the seeds of cacao and coffee are important, and only the oil from the fruit of the African oil palm is utilized.

Few of these fruit are important foods, either locally or globally. Only a dozen or so of the major crop plants worldwide are tropical fruit. Rather than great economic or food importance, they provide dietary variety. They are often nutritious and are usually significant sources of vitamins. They also contain important minerals and carbohydrates, and some, such as avocado, are uncommon botanical sources of fat.

To the nutritional and organoleptic attributes of tropical fruits one must add their monetary value and international significance. The annual production of six of these fruit exceeds 2 million metric tons, and another dozen or so are marketed worldwide (Table 2). In international trade, tropical fruit and their associated products have an aggregate annual value of ca US$20 billion. More significant, however, is their value in local markets and situations.

Crop	**Total production (MMT)[b]**	**Export production**	
		Quantity (MMT)[b]	**Value (millions US$)**
Citrus, mainly *Citrus* spp.[u]	104.78	13.35 (12.7%)	8,655
Banana, *Musa* spp.[v]	89.44	15.1 (16.9%)	4,835
Coconut, *Cocos nucifera*[w]	48.15	2.59 (5.4%)	1,319
Mango, *Mangifera indica*[x]	25.0	0.61 (2.4%)	397
Pineapple, *Ananas*	13.26	2.47 (18.6%)	1,818

comosus[y]			
Papaya, *Carica papaya*	5.23	0.14 (2.7%)	90
Avocado, *Persea americana*	2.22	0.28 (12.6%)	361
Passion fruit, *Passiflora* spp.	1	n/a	n/a
Carambola, *Averrhoa carambola*	0.5	n/a	n/a
Tropical fruit[z]	n/a	0.13	93

[t]Production figures are in millions of metric tons.
[u]Includes fruit of all *Citrus* species, their hybrids, and kumquat (*Fortunella* spp.), a citrus relative. Export figure is for fresh fruit, fruit products, juice and juice concentrate.
[v]Includes both banana and plantain, which is a type of banana. Export figure is for fresh fruit only.
[w]Export figure is total for coconuts, coconut cake, desiccated coconut, coir, copra and coconut oil.
[x]Export figure is total for fresh fruit, juice and pulp.
[y]Export figure is total for canned fruit, fresh fruit, juice and juice concentrate.
[z]Export figure is total for fresh fruit of several different crops for which individual production figures are not available.

Table 1. 1999 production statistics for major tropical fruit crops[t]

Only small percentages of most tropical fruits are exported outside the producing countries. About 2.5% of all mangos and papayas are exported, and exported quantities of other important tropical fruit, such as durian and mangosteen, are probably lower. In some cases, processed products are significant. For example, more pineapple is shipped in cans than as intact fruit, and about one-third of all citrus fruit is processed as juice.

The most notable tropical fruit is banana. Over 100 million metric tons are produced annually, and it is the world's fourth most valuable food after rice, wheat and milk (more citrus fruit are produced, but their total value is lower). As for most tropical fruit, a relatively small percentage of the bananas that are produced every year is exported. About 85% of the harvested total is consumed in the producing countries. For many people in Africa, the Americas and Asia, banana is a staple.

	Order	**Family (subfamily)**	**Crop(s), taxa**	**Center of origin**[v]	**Major production areas**
Magnoliid complex	Laurales	Lauraceae	avocado, *Persea americana*	Tropical America	Mexico, USA, Indonesia, South Africa, Chile
	Magnoliales	Annonaceae	*Annona* spp., cherimoya, ilama, soursop, sugar apple, custard apple; *Rollinia pulchrinervis*, biriba	Tropical America	Tropics
Monocots	Arecales	Arecaceae (Palmae)	peach palm, *Bactris gasipaes*	Central America	Tropical America
			coconut, *Cocos nucifera*	Southeast Asia	Philippines, Indonesia, India, Sri Lanka
			date, *Phoenix dactylifera*	N. Africa, Middle East	Iraq, Iran, Egypt
	Poales	Bromilaceae	pineapple, *Ananas comosus*	South America	Thailand, Philippines, Brazil
	Zingiberales	Musaceae	banana[y], *Musa* spp.	Southeast Asia	Tropical America, Africa
Eudicots (tricolpates)	Caryophyllales	Cactaceae	pitaya	Tropical America	Vietnam, Tropical America
	Oxalidales	Oxalidaceae	carambola, *Averrhoa carambola*	Southeast Asia	Tropics
	Malpighiales	Malpighiaceae	Barbados cherry, *Malpighia glabra*	West Indies, South America	Tropical America
		Clusiaceae [aka Guttiferae]	mangosteen (*Garcinia mangostana*	Southeast Asia	Asia
		Passifloraceae	passionfruit, *Passiflora* spp.	Tropical America	Tropical America
	Rosales	Rosaceae	loquat, *Eriobotya japonica*	China	Subtropics, tropical highlands
		Moraceae	breadfruit, chempedak, jackfruit, etc., *Artocarpus* spp.	Polynesia	Polynesia
			fig, *Ficus carica*	Southern Arabia	Turkey, Egypt, Greece, Iran, Morocco
	Myrtales	Myrtaceae	Surinam cherry et al., *Eugenia*	Tropical America	Tropics

			spp.		
			jaboticaba, *Myrciaria cauliflora*	Brazil	Tropical America
			guava, *Psidium guajava*	Tropical America	global
	Brassicales	Caricaceae	papaya, *Carica papaya*	Central America	Brazil, Nigeria, India, Mexico, Indonesia
	Malvales	Malvaceae	durian, *Durio zibenthinus*	Southeast Asia	Southeast Asia
	Sapindales	Sapindaceae	longan, *Dimocarpus longan*, lychee, *Litchi chinensis*, and rambutan, *Nephelium lappaceum*	Southeast Asia	Tropics
		Rutaceae	citrus, *Citrus* spp.	Southeast Asia	USA, Brazil
		Anacardiaceae	cashew, *Anacardium occidentale*	tropical America	tropical America
			mango, *Mangifera indica*	India, Southeast Asia	India, China, Mexico, Thailand, Pakistan
			Hog plum, mombins, *Spondias* spp.	tropics	tropics
	Ericales	Sapotaceae	Caimito, *Pouteria caimito*	South America	Tropical America
			Sapodilla, *Manilkara zapota*	Central America	Tropical America
			Mamey sapote, *Pouteria sapota*	Mexico, Central America	Tropical America
		Actinidiaceae	kiwifruit (Chinese gooseberry), *Actinidia deliciosa*	Southern China	New Zealand, Chile
		Ebenaceae	persimmons, *Diospyros* spp.	diverse	global
	Solanales	Solanaceae	naranjilla, *Solanum quitoense*	South America	South America

[x] Taxa are listed based on their phylogenetic relatedness.
[y] Probable center of origin in which the crop evolved and primary center of diversity occurs.
[z] Includes plantains, as well as dessert and cooking bananas.

Table 2. Taxonomy, origins and production zones of the major crop plants[u]

2. Significance of Diseases

Diseases are often the most important constraint to the production of tropical fruit. They indirectly reduce yields by debilitating the plant, and directly reduce the yield or quality of fruit before and after they are harvested. They range from esthetic problems that lower the marketability of the harvested product to lethal problems that devastate local or regional production.

Virtually every important tropical fruit is affected by one or more serious diseases. Diseases determine how and where a crop is produced, what post-harvest treatments are utilized, in what markets the crops are sold, and whether production is sustainable and profitable.

3. General Categories of Plant Pathogens

Infectious diseases of plants, i.e., conditions that disturb or harm their normal growth or development, are caused by diverse pathogens. Among the prokayotes, i.e., organisms that lack a nucleus or nuclear envelope, only the Domain Eubacteria contains plant pathogens; none are known in the Archaea (formerly the “archaebacteria”) (Figure 1). Pathogens in the Eubacteria include single-celled microbes without cell walls (the Mollicutes), or with Gram-positive (the Firmicutes) or Gram-negative cell walls (the proteobacteria). The Eubacteria are more phylogenetically diverse than the relatively complex pathogens in the Domain Eukaryota (there is inverse correlation between genome size and an organism’s ability to evolve). However, those in the Eukaryota predominate as plant pathogens. They include an array of multicellular life forms, including fungi, fungus-like oomycetes, nematodes, parasitic plants and protozoa.

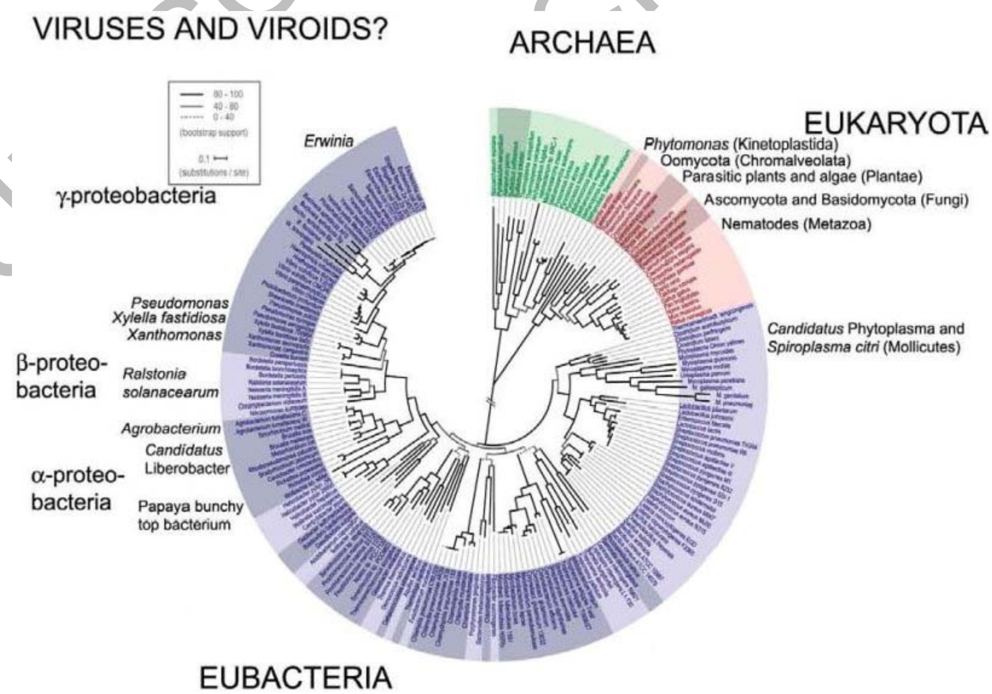

Figure 1. Phylogenetic placement of different groups of plant pathogens. Groups are superimposed on a tree of life that was generated for 191 taxa and 31 genes for which

lateral gene transfer had not occurred. Amended from fig. 2 in Ciccarelli et al. 2006 with permission from Peer Bork.

A third group of pathogens, referred to here as nucleic acid-based pathogens, have unclear affinities to the above life forms. Viruses are single- or double-stranded RNAs or DNAs that are usually encased in protein or lipoprotein envelopes. They are simple pathogens, with genomes of a few thousand to a million nucleotides (nt) that encode 1 to 12 proteins; they replicate only within living cells of their hosts. Even simpler are the viroids, which are the smallest of all infectious disease agents. They are circular, nonenveloped molecules of a few hundred nucleotides, and a tropical fruit, avocado, is the host of the smallest of these pathogens, *Avocado sunblotch viroid* (246-250 nt).

4. Tropical Fruit Pathogens and the Diseases that they Cause

Fungi are the most prevalent and important plant pathogens. In descending order, significant but less frequent diseases are caused by viruses, bacteria, oomycetes, nematodes, phytoplasmas, viroids, parasitic plants and protozoa. In the following sections are described representative pathogen taxa and the diseases that they cause on tropical fruit. They are listed in the phylogenetic hierarchy that is noted in Figure 1. This list is followed with a brief discussion on disease interactions, and the chapter ends with an overview of the epidemiology and management of these diseases.

Fundamental to understanding these disease problems is the host:pathogen interaction (i.e., the “pathosystem”). The different causal agents can be divided into two categories, generalists and specialists. Generalists impact diverse host taxa. Examples include pathogens that affect seedlings (“damping-off” oomycetes, such as *Pythium* spp., and fungi, such as *Rhizoctonia solani*, are examples) and fruit (such as the soft-rotting γ-proteobacteria in the genus *Erwinia*). There is usually no host resistance to diseases that are caused by the generalists. Host-specific pathogens impact far fewer host species than the generalists. They can often be classified as coevolved or new encounter, based on whether or not they have had an evolutionary history with their host(s) (Table 3). Host resistance to coevolved pathogens is common and has been used extensively in the management of the diseases that they cause. Since host resistance to the new encounter pathogens is available less frequently, managing these diseases often relies on other measures (see below).

	Pathogen (disease)	
Crop	**Coevolved**	**New encounter**
avocado	*Sphaceloma perseae* (scab)	**Phytophthora cinnamomi* (phytophthora root rot)
banana	**Fusarium oxysporum* f. sp. *cubense* (Panama disease), **Mycosphaerella fijiensis* and *M. musicola* (Sigatoka leafspots)	**Ralstonia solanacearum* phylotype II (Moko disease), * *Xanthomonas vasicola* pv. musacearum (xanthomonas bacterial wilt)
citrus		**Candidatus* Liberibacter africanus, *Candidatus* Liberibacter asiaticus and *Candidatus* Liberibacter americanus [huanglongbing

		(greening)]
coconut		*phytoplasmas (lethal yellowing, Awka wilt, coconut lethal disease, etc.), *Bursaphelenchus cocophilus* (red ring), *Phytomonas* (hart rot),
mango	**Fusarium mangiferae* (malformation)	**Fusarium sterilihyphosum* and **Fusarium* sp. (malformation); **Ceratocystis manginecans* (seca, sudden wilt)
papaya		**Papaya ringspot virus* (papaya ringspot), **Phytophthora palmivora* (fruit, root and stem rot), **Candidatus* Phytoplasma australasia (papaya dieback, yellow crinkle and mosaic)
pineapple	**Fusarium guttiforme* (fusariosis)	

Diseases marked with an asterisk are serious production constraints.

Table 3. Selected coevolved and new encounter pathogens of tropical fruits.

4.1. Eukayota

About three times as many plant pathogens are eukaryotes than are the prokaryotic and nucleic acid-based pathogens combined. Eukaryotic pathogens utilize diverse ecological niches, reproductive strategies and life styles, and cause a wide range of symptoms on many hosts and host organs.

4.1.1. Kinetoplastida

Uniflagellate protozoans in the genus *Phytomonas* (Kinetoplastida, Trypanosomatidae) are rare plant pathogens. They are found in a variety of tissues, but cause disease only in some hosts. To distinguish different strains, recognition of the following sections was suggested: phloemicola, for phloem-restricted isolates; laticicola, for laticifer-inhabiting isolates; and frugicola, for those from fruit or seed. Isolates in sections laticicola and frugicola are genetically diverse and do not appear to be plant pathogens. For example, frugicola isolates from annona, citrus and mango are not associated with symptoms on these hosts. In contrast, genetically uniform isolates of *Phytomonas* sp. (formerly *staheli*), section phloemicola, cause hartrot, a lethal disease of coconut and African oil palm in tropical America.

4.1.2. Chromalveolata

Some of the most important plant pathogens are members of the Stramenopila (Chromalveolata). These microbes are related to diatoms and brown algae, and are commonly known as "water molds" since the diseases they cause are prevalent in wet environments. Although they resemble fungi, they have diploid, coenocytic, vegetative hyphae, and cell walls that are made primarily of cellulose, rather than the chitin that true fungi possess.

Species in the Pythiaceae (Oomycota) are the most significant tropical fruit pathogens. They cause root rots, trunk cankers, foliar blights and fruit rots, and produce a variety of propagules including chlamydospores, hyphal swellings, oospores (sexual spores that require compatible mating types in heterothallic species), sporangia and motile zoospores.

Pythium spp. are usually generalists that cause root diseases on a wide range of hosts. They can kill seedlings and small plants, or cause significant losses of feeder and structural roots (Figure 2). They are problems on virtually every tropical fruit in Table 2.

Figure 2. Root rot, caused by *Pythium splendens*, has weakened the structural roots of this atemoya (*Annona squamosa* x *A. cherimola*) sufficiently to allow the plant to be pulled easily from the soil.

In contrast, *Phytophthora* spp. are usually somewhat host-specific. They also kill seedlings, but are more serious problems on adult plants, usually causing root rots, trunk cankers and fruit rots. Five important species of *Phytophthora* are listed below.

P. cinnamomi is an uncommon member of the genus in that it affects over 1,000 species of plants. Since it originated in New Guinea, virtually all of its hosts are new encounters. The tropical fruit hosts include cherimoya, kiwifruit and pineapple, and it is the most important pathogen of avocado (Figure 3). *P. cinnamomi* produces distinctive corraloid mycelium. Its nonpapillate, noncaducous sporangia are elliptical to ovoid, but are rarely formed in culture. Terminal and intercalary chalmydospores are abundant in culture and hyphal swellings can also be abundant. *P. cinnamomi* is heterothallic. Its minimum temperature for growth is 5-15^{o}C, the optimum is between 20 and 32.5^{o}C, and the maximum is 30 to 36^{o}C.

Figure 3. The severity of phytophthora root rot of avocado, caused by the new encounter pathogen *P. cinnamomi*, is increased dramatically in flooded soil. These plants have been flooded for 2 weeks. Those on the left are in noninfested soil and those on the right are in soil infested with *P. cinnamomi*.

P. citricola causes diverse diseases of avocado, fig, guava, kiwifruit and mango. It causes trunk cankers on avocado genotypes that have been selected for resistance to *P. cinnamomi*. It produces noncaducous sporangia that vary from obovoid, obclavate and obpyriform to slightly flattened on one side. They are semipapillate and can have a single apex or be deeply bifurcated with two apices, or irregularly shaped with three or four apices. Chlamydospores are rare. *P. citricola* is homothallic. Its cardinal temperatures for growth are 3, 25-28, and 31^{o}C.

P. citrophthora affects chempedek, citrus and kiwifruit. It produces variable, noncaducous sporangia. They range in shape from spherical, ovoid, obpyriform, obturnate, ellipsoidal to extremely distorted. They are persistent, mostly papillate, and often have two or more papilla. Chlamydospores are uncommon for isolates from citrus, and sex organs do not occur in nature although oospores can be induced when some isolates are paired on carrot agar. Its cardinal temperatures for growth are <5^{o}C, 24-28^{o}C, and 32-33^{o}C.

P. nicotianae (aka *P. parasitica*) causes fruit, heart and root rots on carambola, fig, pineapple, rambutan and sugar apple. It forms noncaducous ellipsoid, ovoid, pyriform to spherical sporangia with usually a single papillum. They are produced either singly or in sympodia on stalks. The pathogen forms intercalary and terminal chlamydospores, and most isolates are heterothallic. Its cardinal temperatures for growth are 5-7^{o}C, 27-32^{o}C, and 37^{o}C.

P. palmivora is a ubiquitous pathogen in the tropics with a wide host range. It causes bud, crown, fruit, heart and root rots of atemoya, avocado, breadfruit, coconut, durian, fig, longan, mango, papaya, pineapple, pond apple and soursop. Its hyphae are often irregular and sporangia are prominently papillate and caducous with long pedicels. Chlamydospores are formed by most isolates. *P. palmivora* is heterothallic and its cardinal temperatures for growth are 11, 27.5–30, and 35^{o}C.

4.1.3. Plantae

Parasitic plants, such as mistletoes, dodder and broomrape, are usually not important plant pathogens. A green alga, *Cephaleuros virescens* (Algae, Chlorophyta, Trentepholiaceae) is the most common of these pathogens on tropical fruits. It causes algal leafspot (red rust) on avocado, breadfruit, carambola, citrus, durian, longan, lychee, mango, mangosteen and rambutan (Figure 4). The algal thallus is orange to rust colored and develops below the host cuticle. It produces sporangia on the terminals of erect stalks which produce biflagellate zoospores. Flask-shaped gametangia that are responsible for sexual reproduction are also formed in the thallus. Gametangia release biflagellate gametes in free water, which fuse in pairs to produce sporophytes.

Figure 4. Algal leafspot (red rust) on mango and many other tropical fruit crops is caused by the green alga, *Cephaleuros virescens*. The algal thallus is orange to rust colored and develops below the host cuticle under wet conditions.

Algal leafspot is usually serious only in poorly managed orchards. In these situations mites, insects and other foliar diseases can increase the severity of the disease. Algal leafspot requires a humid environment to establish and spread. The alga's zoospores are the primary infective propagules, and they are dispersed by rain splash and wind.

4.1.4. Fungi

The Kingdom Fungi has been traditionally comprised of four groups, the Ascomycota, Basidiomycota, Chytridiomycota and Zygomycota. Recent phylogentic work indicates that the Chytridiomycota and Zygomycota are not monophyletic groups. Relationships among their members need further clarification, and they are not discussed further since their members cause minor problems. The Ascomycota and Basidiomycota are monophyletic and have been merged into the Subkingdom Dikarya; it contains more tropical fruit pathogens than all other pathogen groups combined.

Ascomycota

***Botryosphaeria* spp.** Several important pathogens of tropical fruits have *Botryosphaeria* teleomorphs (Botryospaeriaceae, Botryospaeriales, Dothidiomycetes, Pezizomycotina). They produce uni- or multi-locular ascomata with multi-layered dark walls, singly or in clusters, and are often immersed in stroma. Some of the pathogens do not produce teleomorphs, but have been associated with this genus via molecular analyses. The associated anamorphs have been divided into two groups. One contains *B. rhodina* and *Diplodia*, *Lasiodiplodia* and *Sphaeropsis* anamorphs that produce conidia that are light to dark brown when mature and usually >10 μm in width. The other includes *B. dothidea* and *Fusicoccum* anamorphs that produce conidia that are usually <10 μm in width and hyaline.

B. rhodina (anamorph: *Lasiodiplodia theobromae*) is one of the most common plant pathogens in the tropics. It causes diverse fruit, foliar and branch diseases on *Annona* spp., *Artocarpus* spp., avocado, banana, carambola, durian, longan, lychee, mango, mangosteen and rambutan. *B. rhodina* produces fluffy, grey to black mycelium on oatmeal agar (OA) and potato dextrose agar (PDA).

B. rhodina attacks trees that are weakened by extreme temperatures, drought and other factors. It infects through wounds, and causes symptoms on fruit as they ripen. It is often an endophyte (i.e., colonizes host tissue without causing symptoms), and can also be found in soil, on dead twigs, mummified fruit and on organic debris beneath trees.

***Ceratocystis* spp.** The genus *Ceratocystis* (Microascales, Hypocreomycetidae, Sordariomycetes) includes plant pathogens that cause a wide range of symptoms. They are found on woody and herbaceous hosts, often in the tropics. Many are vectored by flying insects. They produce brown to black perithecia with long necks that exude ascospores in a sticky matrix.

C. paradoxa (anamorph: *Thielaviopsis paradoxa*) is prominent on tropical fruit, and causes butt rot, fruit rot and a leaf spot of pineapple, stem bleeding of coconut; foot rot of fig; fruit rot of carambola; and black scorch, inflorescence blight, bud rot, heart rot and trunk rot of date palm. Conidia, which are also called endoconidia, and chlamydospores, are hyaline to slightly brown, cylindrical to slightly oval, and are extruded through the end of the conidiophore. Chains of thick-walled chlamydospores are produced in older cultures, and perithecia and ascospores are produced only occasionally.

Another species, *C. fimbriata* (anamorph: *Thielaviopsis* sp.), the first described in the genus, has been reported on *Annona* spp., *Citrus* spp., fig and mango. It differs from *C. paradoxa* by its longer conidia, nonornamented perithecia and hat-shaped ascospores. Recent work has shown that *C. fimbriata* is a species complex, and that host specialization may have occurred in it several times. For example, isolates that cause lethal diseases of mango in Brazil (seca), Oman (sudden decline) and Pakistan are distinct, and those from Oman and Pakistan have been recently described as a new species, *C. manginecans* (Figure 5). Recognition of these host-adapted populations will assist disease management and quarantine objectives.

Figure 5. The new encounter disease known as sudden decline in Oman is caused by *Ceratocystis manginicans* and vectored by the scolytid beetle, *Hypocryphalus mangiferae* (upper left). Vascular streaking caused by the disease and galleries of *H. mangiferae* are at the lower left, and unilateral death of portions of affected trees in Oman is on the right.

***Fusarium* spp.** Before molecular tools became available, *Fusarium* [(Hypocreales, Hypocreomycetidae, Sordariomycetes (formerly, the “pyenomycetes”)] was a taxonomically difficult genus. Most problematic were taxa that did not produce teleomorphs (some are associated with *Albonectria*, *Gibberella* or *Haematonectria* spp.), since they lacked distinguishing anatomical features. Due to their importance, two groups are discussed below.

The *Fusarium oxysporum* complex (FOC) includes saprophytes (most common), as well as human and plant pathogens. It is a common soil inhabitant, and members do not produce a teleomorph. Among the plant pathogens are host-adapted, coevolved forms, the formae speciales. The most important ff. spp. cause vascular wilt diseases, the fusarium wilts, and several tropical fruit crops are affected (e.g. banana [f. sp. *cubense*], citrus [f. sp. *citri*], date [f. sp. *albedinis*] and passion fruit [f. sp. *passiflorae*]). These diseases occlude the xylem and are difficult to control; host resistance is most useful.

The *Gibberella fujikuroi* species complex (GFSC) contains several distinct mating populations (MPs) that can be distinguished via sexual compatibility and the formation of perithecia. Molecular work has identified related taxa that do not produce teleomorphs, and the tropical fruit hosts include banana (crown rot and pseudostem heartrot), fig (endosepsis), mango (malformation) (Figure 6), and pineapple (fruitlet core rot and fusariosis).

Figure 6. Mango malformation, caused by a member of the *Gibberella fujifuroi* species complex (GFSC) that does not form a teleomorph, *Fusarium mangiferae.* This disease is also caused by other fungi in the GFSC, including *F. sterilhyphosum* and an unnamed mating population in Brazil. The disease is vectored by a phytophagous mite, *Aceria mangiferae*, the only known example of a plant-feeding mite vectoring a plant-pathogenic fungus.

***Glomerella* spp.** *Glomerella* spp. (Glomerellaceae, Melanosporales, Hypocreomycetidae, Sordariomycetes) are among the most common and important above-ground pathogens of tropical fruit. They are facultative saprophytes and common endophytes that cause anthracnose diseases on fruit, leaves and twigs. Two species are described here.

G. cingulata (anamorph: *Colletotrichum gloeosporioides*) has a very wide host range. It causes significant problems on *Annona* spp. avocado, breadfruit, carambola, citrus, durian, fig, guava, jackfruit, lychee, mango, mangosteen, papaya, passion fruit and rambutan (Figure 7). It is most important as a fruit pathogen, but also causes branch and leaf diseases.

Figure 7. Anthracnose, caused by *Glomerella cingulata* (anamorph: *Colletotrichum gloeosporioides*) is the most serious disease of mango in the humid tropics.

On PDA, colonies are whitish to dark grey with thick to sparse lawns of aerial mycelium. Conidia are hyaline, one celled, and cylindrical with obtuse ends. They form on light brown conidiophores in irregular acervuli, and upon maturity appear orange and slimy en masse. Acervuli develop in lesions on leaves, branches and fruit, and conidia in acervuli remain viable for long periods, even under adverse climatic conditions. The fungus is heterothallic and although the teleomorph can be readily induced in culture, it is observed rarely in the field. Appressoria are usually lobed.

Conidia of *C. gloeosporioides* are epidemiologically important. They are produced on virtually all host tissues and are usually dispersed by rainsplash. Moderate temperatures (25 to 30^{o}C) and free moisture are needed for optimum production, germination and infection. New leaf flushes are most susceptible. Although fruits can be infected at any stage of development, infections that occur before ripening usually progress no further than the formation of appressoria. Disease development usually commences after ripening begins.

G. acutata (anamorph: *Colletotrichum acutatum*) affects avocado, breadfruit, carambola, citrus, fig, guava, kiwifruit, lychee, mango and papaya. It causes anthracnose primarily on fruit, and is usually less important than *G. cingulata*. It is also responsible for a serious fruit set disease on citrus, postbloom fruit drop.

Colonies are effuse, white becoming pale orange then greenish grey or black, often with a pink or reddish purple underside. Conidia are hyaline, one celled, straight, smooth, fusiform, and salmon-colored en masse. Appressoria are sparse, mostly light to medium brown, clavate to obvate with smooth margins. Acervuli are superficial to subcuticular. *C. acutatum* differs from *C. gloeosporioides* in its orange to pink colony coloration during the first few weeks of growth, its fusiform conidia and spherical, rather than lobed, appressoria. The fungus is heterothallic, but perithecia have not been observed in the field.

***Mycosphaerella* spp.** *Mycosphaerella* (Mycosphaerellaceae, Capnodiales, Dothidomycetes) contains more than 3,000 named species, making it the largest genus of ascomycetes. At least 23 different genera of anamorphs have been associated with teleomorphs in the genus. They produce small, black, pseudothecial ascomata immersed in host tissue, either singly and superficially, or in a pseudoparenchymatal stroma.

Mycosphaerella spp. are either saprophytes, weak pathogens, or cause serious diseases. The plant-pathogenic species are host-specific and usually restricted to a single genus or family. Host range plays an important role in species identification. Three species that are found on banana are discussed below.

M. fijiensis (anamorph: *Pseudocercospora fijiensis*) causes black Sigatoka (aka black leaf streak); it is the most damaging foliar disease of banana and is found throughout the humid tropics (Figure 8). Its control is a major expense for producers of export bananas, who rely on the highly susceptible Cavendish subgroup of cultivars. It has replaced *M. musicola* (anamorph: *Pseudocercospora musicola*), cause of Sigatoka or yellow Sigatoka, as the most important foliar pathogen of banana. The two pathogens are distinguished by examining the conidia of their anamorphs: those of *Pseudocercospora fijiensis* have a thickened hilum at their base, whereas those of *Pseudocercospora musicola* do not. The recently recognized *M. eumusae* (anamorph: *Pseudocercospora eumusae*) causes eumusae leaf spot. Its symptoms mimic those of black Sigatoka and, as a result, it has an unclear host range, impact and distribution (it appears to be restricted to the Eastern Hemisphere).

Figure 8. *Mycosphaerella fijiensis* (anamorph: *Pseudocercospora fijiensis*) causes the most serious disease of banana, black Sigatoka (aka black leaf streak).

***Rosellinia* spp.** *Rosellinia* spp. (Xylariaceae, Xylariales, Xylariomycetidae, Sodariomycetes) produce superficial perithecia on host bark, usually in dense swarms of hyphae. Asci are unitunicate with an apical ring, ascospores are black and unicellular. Three types of species are recognized: strict saprophytes, endophytes that are occasionally pathogenic, and severe root pathogens. Three in the later group are important on tropical crops.

R. necatrix (anamorph: *Dematophthora necatrix*) causes white root rot on avocado, cherimoya, citrus, fig and kiwifruit. The rare teleomorph has spherical, black perithecia that are embedded in mats of brown hyphae. Conidiophores of the more common anamorph are produced on brown, ropey, rigid synnemata composed of intertwined, laterally cemented hyphae. Conidia produced on synnemata are one-celled, solitary, elliptical to ovoid, colorless to pale brown and smooth. Peculiar pear-shaped swellings often occur near the septa on the hyphae, especially on older hyphae. The fungus also produces scattered, black, rough, irregular masses of microsclerotia that often unite to form irregular, flattened masses or sheets that enable long-term survival. Feeder roots are directly infected when they contact hyphae or microsclerotia. The infection spreads into woody roots and may spread from tree to tree in this manner.

Two other species cause black root rot of avocado, banana and citrus in the tropics. *R. bunodes* (anamorph: *Dematophora* sp.) is widespread in tropical America and in various locations in the east. *R. pepo* (anamorph: *Dematophora* sp.) is less widespread in the west and Africa. Black root rot is particularly important in acidic soils with high organic matter content; because the responsible species have wide host ranges and persist in colonized organic debris, it can be difficult to manage.

Basidiomycota

***Armillaria* spp.** *Armillaria mellea* (Physalacriacaeae, Agaricales) causes root rot on avocado, cherimoya, fig, kiwifruit, lychee and soursop. It forms a number of structures including basidiomes (mushrooms), basidiospores, mycelia, white mats or plaques between the bark and wood, pseudosclerotial tissue and rhizomorphs (brown-to-black, cylindrical fungal strands that look somewhat like roots) on the surface of infected roots. Infected tissues have a distinct mushroom odor when moist. Basidiomes are often produced around the base of affected trees after rainfall, but have no known role in the disease cycle.

A. mellea is sometimes referred to as the honey mushroom or shoestring fungus. Its wide host range and ability to survive as a saprophyte make it a difficult pathogen to control. Infection results when roots contact infected plants or rhizomorphs of the fungus in the soil. Infected tree stumps and large roots of dead hosts are common sources of inoculum, and the fungus may persist saprophytically for 10 or more years.

Erythricium salmonicolor. *Erythricium salmonicolor* (anamorph: *Necator decretus*) (Corticiales, Agaricomycetes, Agaricomycotina) causes pink disease on a wide range of tropical crops including breadfruit, carambola, citrus, custard apple, durian, jackfruit, mango, mangosteen and rambutan. Distinct forms of the fungus occur on affected trees. The first, cobweb stage develops as a layer of vegetative mycelium under wet conditions. Eventually, the necator stage develops in which orange sporodochia and conidia of the anamorph are produced. It is followed by the pink incrustation stage of the teleomorph that produces basidiospores. Both conidia and basidiospores are infective and spread by wind.

Pink disease is most important under high rainfall, tropical conditions, and serious damage occurs only in areas where rainfall exceeds 2000 mm per year. The fungus penetrates intact or wounded bark and eventually kills the cambial layer. Ultimately, large diameter branches and entire trees can be killed.

***Ganoderma* spp.** Over 200 species of *Ganoderma* (Ganodermataceae, Polyporales, Agaricomycetes, Agaricomycotina) have been described. Most of these are from temperate areas, but some affect trees in the tropics. They cause white rots and basal cankers, and produce conspicuous conks (fruiting structures) that have a varnished appearance on the upper surface (pileus) (Figure 9). The ovoid, golden basidiospores are distinctive, but have an unclear role in disease transmission on most hosts.

There is some confusion over the identity and importance of the tropical plant pathogens in the genus. *G. tornatum* is apparently the most common species in the tropics, and causes heart rots and basal stem rots. *G. applanatum* affects a wide host range of Gymnosperm and Angiosperm trees in northern latitudes, but has also been reported to cause butt rot on avocado and concentric canker on citrus. Basal stem rot of coconut palm is caused by *G. boninense* in Southeast Asia and *G. zonatum* in the

Eastern and Western Hemispheres; the later species also causes butt rot on avocado. *G. philippi* causes red root rot of mangosteen.

Figure 9. Several species of *Ganoderma* affect tropical fruit crops. By the time conks (fruiting structures at the base of this palm) develop, these pathogens have caused considerable internal damage to their host.

Rigidoporus **spp.** *Rigidoporus* spp. (Meripilaceae, Polyporales, Agaricomycetes, Agaricomycotina) cause white rots of roots and trunk bases of wide range of hosts. *R. ulmaris* and *R. vintus* affect avocado. *R. lignosus* affects carambola, durian and mango, and is probably restricted to Africa and Asia. Its large host range of woody perennials contains other important crops, including rubber, on which huge losses have been reported.

R. lignosus produces white rhizomorphs on the surfaces of roots and root crowns which later darken to a yellowish and then reddish color. The leading edge of the rhizomorph is well-defined and seldom appears above ground. It undergoes a morphogenic change to produce infectious hyphae that penetrate the host epidermis and, subsequently, degrade host lignin. The fungus is most damaging if orchards are established in old rubber plantations or newly cleared jungle sites. Previously colonized stumps and infected woody debris of rubber and other hosts are primary sources of inoculum. Orange-yellow, bracket-like sporophores are produced during the rainy season on the root collar, trunk or exposed roots. Basidiospores produced on the sporophores are viable, and are thought to play a secondary role in disseminating the disease; at most, they probably colonize exposed stump surfaces. Rhizomorphs are more significant epidemiologically, since they grow rapidly and can advance great distances in soil in the absence of woody substrates. The most effective means for controlling white root rot rely on eliminating or avoiding colonized woody debris when new orchards are established.

4.1.5. Metazoa (the Animal Kingdom)

Nematodes (Metazoa, Eumetazoa, Bilaterans, Ecdysozoa, Secernentea, Nematoda) are the second most diverse group of animals after the arthropods. They are nonsegmented roundworms, and the plant pathogenic species have stylets, needle-like mouthparts that allow them to puncture plant cells and extract their contents. Most of the pathogens are soilborne root parasites that can be divided into endoparasites that cause root knots and cysts, enter the host, and feed within the root, and ectoparasites that cause general lesions and necrosis by feeding externally on root surfaces. Ten to 15 % of some crops are lost annually to these pathogens.

There are ca 2,000 species of plant pathogenic nematodes. Most are in the order Tylenchida. With two exceptions, the tropical fruit pathogens are restricted to three families in the suborder Tylenchina, superfamily Tylenchoidea: Pratylenchidae, Hoplolaimidae and Heteroderidae. Exceptions are the sedentary endoparasite *Tylenchulus semipenetrans* (Tylenchina, Tylenchoidea, Criconematoidea, Criconematidae, Tylenchulidae), cause of slow decline of citrus, and the red ring pathogen of coconut, *Bursaphelenchus cocophilus* (Aphelenchina, Aphelenchoididae).

Pratylenchidae. Two genera of important migratory endoparasites are found in this family. They puncture epidermal root cells, eventually colonize the root cortex, and can cause significant root necrosis alone and in combination with other pathogens. Lodging can occur in plants with severely damaged root systems.

Lesion nematodes, *Pratylenchus* spp., are the most prevalent fruit pathogens in this family. *P. brachyurus* is an important pathogen of pineapple and causes minor problems on citrus; *P. coffeae* is important on banana, but is minor on citrus and pineapple; *P. goodeyi* is also important on banana, but is found only in the Canary Islands and Africa.

The burrowing nematode, *Radopholus similis*, is the most important nematode on banana, on which it causes black-head toppling syndrome. It also causes spreading decline of citrus.

Hoplolaimidae. The reniform nematode, *Rotylenchus reniformis*, is found on a wide range of hosts in the tropics and subtropics. It affects papaya and passionfruit, and became a serious problem in Hawaiian pineapple production where chemical fertilizers reduced soil pH.

The spiral nematode, *Helicotylenchus multicinctus*, impacts breadfruit and jackfruit, and is an important problem on banana in subtropical or high elevation tropical production areas; on the later crop it causes less extensive cortical damage than *Pratylenchus* spp. and *Radopholus similis*.

Heteroderidae. The sedentary endoparasitic root knot nematodes, *Meloidogyne* spp., are the most common plant pathogenic nematodes. They are sedentary endoparasites, and usually have wide host ranges. *Meloidogyne* sp. affects breadfruit and jackfruit; *M. arenaria*, banana, date palm, fig, guava, kiwifruit, papaya and passionfruit; *M. hapla*, date palm, kiwifruit and papaya; *M. incognita*, banana, date palm, guava, kiwifruit, papaya, passionfruit and pineapple; *M. javanica*, banana, date palm, guava, kiwifruit, papaya, passionfruit and pineapple; and *M. mayaguensis*, guava. These nematodes can interact synergistically with other pathogens.

4.2. Eubacteria

The Eubacteria are phylogenetically diverse and include serious plant pathogens. Below are brief descriptions of some of the important tropical fruit agents.

4.2.1. Firmicutes (bacteria with Gram positive or no cell walls)

The Firmicutes include Eubacteria without cell walls, the Mollicutes, and those with Gram-positive cell walls; the later are not important on tropical fruits.

Mollicutes include the phytoplasmas, unculturable pathogens in the order Acholeplasmatales. The genus "*Candidatus* Phytoplasma" has been created to accommodate members of this important group. Taxa in the genus include agents that are associated with, and presumably cause: yellow crinkle and mosaic of papaya; dieback of papaya; witches' broom disease of limes (Figure 10); diverse yellowing disorders of palm, especially coconut; phytoplasma-associated diseases of date palm. *Spiroplasma citri* (Spiroplasmataceae) is the culturable cause of citrus stubborn disease.

Figure 10. Lime witches' broom is one of several serious new encounter diseases of citrus (here on *Citrus aurantifolia*). Found in the Middle East and associated with a phytoplasma, it initially dwarfs and malforms terminal portions of the canopy (upper figure), and later kills large portions of the tree (lower figure).

4.2.2. Proteobacteria (Gram negative bacteria)

Tropical fruit pathogens are found in three divisions of proteobacteria. The α-proteobacteria includes the well-known crown gall pathogen, *Agrobacterium tumifaciens*. It affects a wide range of dicots. Also in the α-proteobacteria are the putative huanglongbing (greening) agents of citrus: *Candidatus* Liberibacter asiaticus, which was restricted to Asia, but detected recently in Florida; *Candidatus* Liberibacter africanus, found only in Africa; and *Candidatus* Liberibacter americanus, recently described in Brazil. Huanglongbing is a destructive new encounter disease which is difficult to manage; it eliminates commercial production of citrus shortly after it becomes widely established in most areas. The probable cause of a serious disease of papaya in the Caribbean region, papaya bunchy top, was recently reported to be an unculturable relative of the Rickettsia pathogens of animals.

In the β-proteobacteria are serious vascular wilt pathogens in the species complex, *Ralstonia solanacearum*. Phylotype II of *Ralstonia solanacearum* causes Moko, a new encounter disease of banana in tropical America (Figure 11), whereas phylotype IV causes blood disease of banana in Southeast Asia.

Figure 11. Moko, a new encounter disease of banana in tropical America, is caused by phylotype II of *Ralstonia solanacearum*. Some strains of the bacterium are vectored by flying insects to the developing infloresence (note initiation of symptoms on the raceme at the right). Photos courtesy of I. W. Buddenhagen.

Diverse plant pathogens are found in the γ-proteobacteria. They include soft-rotting *Erwinia* spp. that affect fruit (avocado, papaya and passionfruit) and plants (banana, chempedak, guava and pineapple); *Pseudomonas* spp. that cause blossom blight (kiwifruit), leaf spots (mango, passionfruit and papaya) or cankers (avocado, fig); and *Xylella fastidiosa*, which causes citrus variegated chlorosis. Most important, however, are various taxa in *Xanthomonas*: *X. axonopodis* pv. citri causes citrus canker, a serious disease of quarantine significance; *X. axonopodis* pv. *mangiferaeindicae* causes a serious fruit and foliar disease of mango, bacterial black spot; *X. vasicola* pv. musacearum causes a devastating, lethal wilt of banana, xanthomonas bacterial wilt; and *X. campestris* pv. passiflorae causes the most important bacterial disease of passionfruit, bacterial spot.

4.3. Nucleic Acid-Based Pathogens

4.3.1. Viruses

The 14 families and 70 genera of plant viruses are classified based on biochemical composition, replication strategies, particle structure, and genome organization. Tropical fruit are affected by numerous viruses, especially those that are propagated by vegetative means; citrus and passionfruit are notable in the numbers and diversity of viruses that affect them. Representatives from a subset of those that impact these crops are discussed briefly below.

***Potyviridae*.** Members of the *Potyviridae* have flexuous particles 650-900 nm in length, with a positive sense ssRNA genome. Two viruses in the genus *Potyvirus* are important tropical fruit pathogens.

Papaya ringspot virus-type P (PRSV-P) causes papaya ringspot, a limiting factor in papaya production worldwide. PRSV-P virions are 780 x 12 nm and encapsidated with a 36 kDa coat protein. It is transmitted nonpersistently by transitory populations of aphids (papaya is not a preferred host). Tolerance to papaya ringspot is available in some genotypes, but more effective resistance has been produced in a variety of genetically transformed clones; some of the later cultivars saved the papaya industry in Hawaii.

Passionfruit woodiness virus (PWV) is the most serious of the many viruses that affect *Passiflora* spp. [several other potyviruses, as well as species in *Carlavirus* (ssRNA+), *Closterovirus* (ssRNA+), *Cucumovirus* (ssRNA+), *Geminiviridae* (ssDNA), *Rhabdoviridae* (ssRNA-), *Tobamaovirus* (ssRNA+), and *Tymovirus* (ssRNA+) also impact these plants]. Passionfruit woodiness, the most serious virus-induced disease of this crop, has a complicated etiology in that its symptoms, particularly a malformed, thickened and hardened pericarp, are associated with *Cucumber mosaic virus* and several potyviruses, including PWV. PWV virions are 11-15 x 680 – 900 nm with a 9-10 kb genome. It is vectored by aphids and transmitted mechanically and by grafting.

***Closteroviridae*.** Closterovirus virions are long, very flexuous particles. *Citrus tristeza virus* (CTV) causes tristeza decline and stem pitting of citrus, the most serious virus-induced problems on this crop. Over 50 million trees on the sour orange rootstock have been killed, and >200 million trees that remain on this rootstock worldwide are at risk. CTV has 12 x 2000 nm virions and the largest genome of the positive sense ssRNA plant viruses, 19.3 kb. Several aphids transmit CTV in a semi-persistent manner; most effective is the brown citrus aphid, *Toxoptera citricida*.

Mealybug wilt is a serious problem on pineapple worldwide. Only recently has its etiology been understood. In Hawaii, at least three viruses are found in symptomatic plants, but a causal role was only demonstrated for *Pineapple mealybug-wilt associated virus*-2. It, infestations of mealybugs (*Dysmicoccus brevipes* and *D. neobrvipes*), and ants that protected the mealybugs were key in disease development; plants that were only infected or infested did not develop symptoms.

Figure 12. Bunchy top, the most important virus-induced disease of banana, is vectored by the banana aphid, *Pentalonia nigronervosa*, and is probably caused by *Banana bunchy top virus*, a multicomponent nanovirus.

Caulimoviridae. Virions in this virus family have circular, dsDNA genomes, and replicate via reverse transcription. The genus *Badnavirus* contains several viruses that are important in the tropics, and *Banana streak virus* (BSV) is one of the most significant on banana. BSV has bacilliform virions, 30 x 130 – 150 nm in size, with a 7.4 kbp genome. It is vectored by mealybugs, but also spreads in infected germplasm. BSV is highly variable, and several variants are sufficiently diverse to be considered different species. Streak can cause serious losses, and has also affected the dissemination of new banana hybrids and germplasm. Some strains of BSV integrate into the banana genome and can become episomal due to stress, such as tissue culture or meiosis. This has caused serious problems for banana-breeding programs, since virions can be produced in materials previously determined to be "BSV-free."

Circoviridae. This is one of the two families of plant viruses that contain ssDNA. The only plant-associated genus in the family, *Nanovirus*, contains the most important virus pathogen of banana, *Banana bunchy top virus* (BBTV) (Figure 12). BBTV has a multicomponent genome of at least six circular components 1000 – 1100 nt in length. Virions are icosahedrons 18-20 nm in dia. Although BBTV has not conclusively been shown to cause bunchy top, virions are intimately associated with the disease, and are always detected in symptomatic plants. BBTV is vectored by the banana aphid, *Pentalonia nigronervosa*, and is also disseminated in vegetative propagation materials.

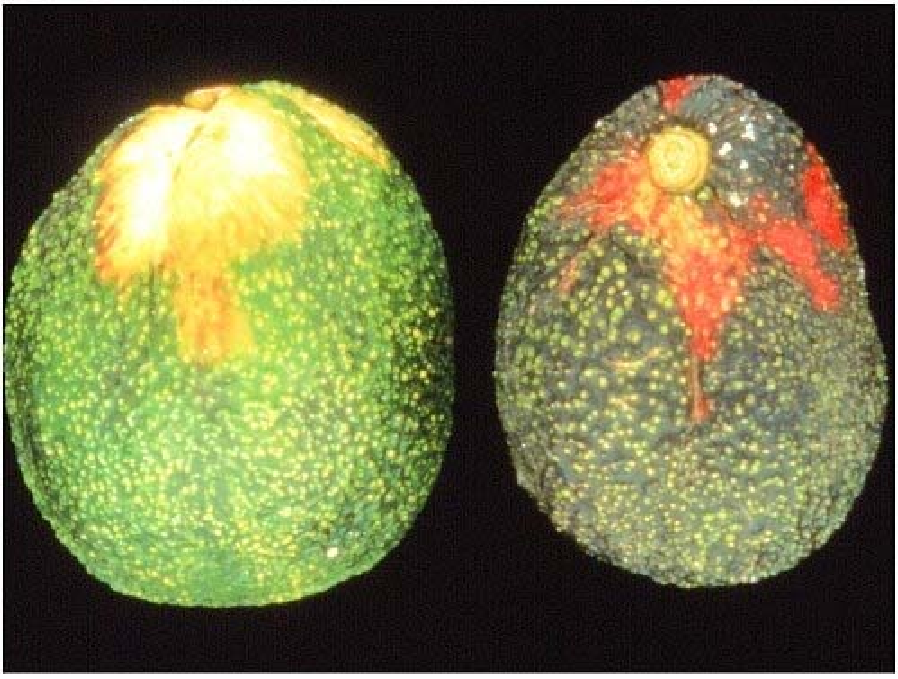

Figure 13. The smallest known plant pathogen, *Avocado sunblotch viroid*, causes color breaks and deformation of avocado fruit. Photo courtesy of G.A. Zentmyer.

4.3.2. Viroids

Two families of this small group of plant pathogens are recognized. In the Pospiviroidae are two serious coconut pathogens in the genus Cocadviroid, *Coconut cadang-cadang viroid,* which is found in the Philippines, and *Coconut tinangaja viroid*, which is found on Guam. The epidemiology of the ultimately lethal diseases they cause are poorly understood. Several viroids in the Pospiviroidae are known in citrus, the most important of which is in the genus Pospiviroid, *Citrus exocortis viroid* (CEVd). CEVd is widespread, but remains symptomless in most scion cultivars. Symptoms are expressed only when infected scions are grafted on sensitive rootstocks, such as trifoliate orange, citranges and 'Rangpur' lime.

Avocado sublotch viroid (ASBVd) is one of only three members of the Avsunviroidae. It stunts trees, deforms fruit, and is transmitted in scion material and root grafts (Figure 13). It also moves in pollen, but only the fruit that it fertilizes is infected.

5. Interactions

Pathogens interact with the environment and the biological world in diverse ways. The epidemiology of tropical fruit disease is addressed in the next section, but two specific aspects are covered briefly here.

Many pathogens rely on external agents to move to or infect tropical fruit. Virus vectors are most common and include mites, nematodes, fungi and a parasitic plant, dodder. However, insects are the most important vectors of viruses, and they include in descending order of importance, aphids (Aphididae), leafhoppers (Cicadellidae), planthoppers (Delphacidae), whiteflies (Aleurodidae), mealybugs (Cocoidae), treehoppers (Membracidae), true bugs (Hemiptera), thrips (Thysanoptera), beetles (Coleoptera), and grasshoppers (Orthoptera). An important general relationship of these pathogens with their vectors addresses how long they persists with, or propagates in, their vector.

Notable examples of tropical fruit viruses that are transmitted by insects include: *Banana bunchy top virus*, which is vectored by the banana aphid, *Pentalonia nigronervosa*, in a circulative, non-propagative manner (Figure 12); *Banana steak virus*, which is transmitted in a semi-persistent manner by mealybugs; *Citrus triztesa virus*, which is vectored by several aphid species, but most effectively by the brown citrus aphid, *Toxoptera citricida*; *Tomato spotted wilt virus*, which is vectored by the western flower thrips, *Frankliniella occidentalis*; and *Passionfruit woodiness virus* and *Papaya ringspot virus*, which are vectored by several different species of aphid.

Vectors also play important roles in the epidemiology of diseases caused by: the hartrot *Phytomonas* sp., vectored by pentatomid (*Heteroptera*) insects in the genera *Lincus* and *Ochlerus*; phylotype II of *Ralstonia solanacearum* and *Xanthomonas vasicola* pv. musacearum, vascular wilt pathogens of banana that are vectored by bees, wasps and other flying insects (Figure 11); the phytoplasmal agents that cause lethal yellowing-type diseases of coconut, vectored by planthoppers; *Bursaphelenchus cocophilus*, the red ring nematode of coconut, vectored by primarily by adults of the American palm weevil, *Rhynchophorus palmarum*; the seca and sudden decline pathogens of mango, vectored by the mycangial beetle, *Xyleborus mangiferae* (Figure 5); a malformation pathogen of mango, *Fusarium mangiferae*, vectored by *Aceria mangiferae* (Figure 6); and phytyoplasmal pathogens of papaya in Australia, probably vectored by leafhoppers or plant hoppers.

An unusual interaction occurs in fig. Fig wasps (Hymenoptera, Chalcidoidea, Agaonidae) have coevolved with fig species as their pollinators. *Blastophaga psenes*, the pollinator of *F. carica*, introduces conidia of endosepsis pathogens inside developing fruit during pollination, most notably *Fusarium lactis*. Parthenocarpic selections of *F. carica* that do not require pollination neither interact with *B. psenes* nor develop endosepsis.

Other pathogen interactions results in altered disease development. For example, canker, caused by *X. axonopodis* pv. citri, and phytophthora root rot, caused by *Phytophthora palmivora*, are diseases of citrus whose severities are increased by, respectively, the citrus leaf miner, *Phyllocnistis citrella*, and diaprepes root weevil, *Diaprepes abbreviatus*, whereas the development of anthracnose of avocado, caused by *Colletotrichum gloeosporiodes*, is increased by scab damage, caused by *Sphaceloma perseae*.

6. Disease Epidemiology and Management

Diseases that impact tropical fruit crops can be significant constraints to production, especially when they occur in lowland environments with high rainfall and uniform, warm temperatures. This topic is introduced with a few concepts on the occurrence and development of these pathosystems. The successful management of plant disease utilizes several principles and practices, regardless of the host and environment in which it is grown. These include the avoidance, exclusion and eradication of the causal agents. Host protection is of great importance, as is the identification and incorporation of resistance in the host plant.

6.1. Epidemiological Principles

Effective management strategies usually rely on an understanding of the disease's etiology and epidemiology. When causal agents are not known, or when they can not be cultured and used to artificially induce disease, it is difficult or not possible to test treatment efficacy. Two debilitating citrus diseases provide examples: blight, which has an unknown etiology, and huanglongbing (greening), which has at least three nonculturable, putative agents. And even when causal agents are known, unclear epidemiologies or an inability to reproduce symptoms artificially with a given agent are significant handicaps. In general, effective disease management relies on a delay in the onset or reduction in the initial levels of disease (x_o), or a reduction in the rate at which disease develops over time (r).

6.2. Avoidance

Planting site selection is an important first step in establishing a production area, and can be an important tactic for disease avoidance. In general, the conditions under which disease development is favored or hosts are predisposed to disease development should be considered. For example, root rots that are caused by oomycetes are exacerbated in low-lying and poorly drained situations (Figures 2 and 3). By avoiding chronically wet sites it is possible to reduce x_o for these diseases, but especially r.

Likewise, production areas in which hosts might be predisposed to disease development should be avoided. Predisposing factors are usually physical, but indirect in their impact. Water and temperature extremes are most often indicated, although optimal temperatures for the host might still lead to enhanced disease if it also favors the pathogen. Physical damage to the host might also predispose it to disease development, and this can be abiotic, as is the case with wind damage and the development of bacterial black spot of mango, or biotic, as for the enhanced development of citrus canker in leaves damaged by the citrus leafminer. Managing the predisposing factors is always helpful.

The importance of using disease-free planting materials cannot be overstated, and any measure that facilitates their production and utilization would be useful. For example, clean nursery stock and budwood schemes are hallmarks of successful citrus programs.

Vegetative propagules can harbor bacteria, fungi, nematodes, viruses and viroids, and it is with them that many economically important pathogens are moved and established.

Tissue-culture plantlets should be used whenever possible, since they are free of fungal, bacterial and nematode pathogens ($x_o = 0$). They are also free of virus and viroid pathogens when they are produced from indexed mother plants. Only in rare cases are tissue-culture plantlets not safe. The badnaviruses, such as *Banana streak virus*, cause exceptional problems (see above).

Many diseases of perennial crops originate in propagation nurseries, and soilborne diseases whose symptoms are not readily apparent can be most problematic. Phytophthora root rot of avocado is a good example (Figure 3). *P. cinnamomi* originated in New Guinea, but has been disseminated worldwide in contaminated planting stock. Its establishment in new orchards usually results when trees that were infected in the nursery are planted.

6.3. Exclusion

Diverse tactics exist for the exclusion of plant pathogens. Although excluding pathogens from production areas ($x_o = 0$) can be a difficult, this is a most cost-effective disease management strategy. Production should begin with pathogen-free germplasm, and its identification/certification can depend on sensitive and accurate pathogen-detection protocols.

Most pathogens require human intervention for long-distance dispersal (LDD). Thus, quarantines can be an important first line of defense against their intended or unintended movement, and most countries have lists of forbidden or restricted pathogens and host plants. Unfortunately, enforcing these rules to ensure border safety is not always possible. The recent accidental introduction of *Xanthomonas axonopodis* pv. citri into citrus-growing areas in Florida and Queensland, Australia are good examples of the accidental dissemination of plant pathogens during the illicit movement of plant material. The removal of trade barriers may also be problematic. For example, the potential movement of nonendemic pathotypes of *Guignardia musae* and *Ralstonia* *solanacearum* into Australia were issues in the campaign against the importation of Philippine bananas into this country.

Pathogens that are moved in debris and on machinery, tools and other implements can be excluded by surface disinfestation with chemical and physical measures. Likewise, seed and planting material can be treated to kill pathogens. Heat treatment (thermotherapy) of vegetative propagation materials is useful against some bacteria, fungi, nematodes and viruses. For example, the burrowing nematode, *Radopholus similis*, can be eliminated from banana suckers by hot water treatment. Some pathogens can be eliminated from true seed, especially if contamination is restricted to the seed exterior. Although heat treatment is also used for this purpose, surface disinfestation with chlorine or fungicides is more common. Pathogen vectors can also be eliminated to exclude pathogens of concern, but this is usually a difficult objective.

6.4. Eradication

If pathogen exclusion has failed or is not possible, other strategies are needed. These measures are diverse, always more expensive than pathogen exclusion, and seldom entirely effective (The recent investment of ca US$1 billion in the failed eradication of citrus canker in Florida is an extreme example.) Although the goal of eradication is to reduce x_o to 0, in practice these measures are most often rate limiting.

When they are significant reservoirs of inoculum, alternative hosts are removed from plantations and destroyed. Disease pressure is usually reduced in such cases, especially when pathogen host ranges are limited. The effectiveness of removing alternative hosts depends on their size (is accomplished most readily when plants are small enough to be easily uprooted and removed) and the pathogen's mobility.

The removal of infested debris and host materials is another common eradication strategy. As above, its impact depends upon the ease with which these reservoirs of inoculum can be removed from plantations. Roguing infected plants is a key strategy, especially if the crop plant is the primary or sole source of inoculum. For example, bunchy top of banana, caused by *Banana bunchy top virus*, can be managed only if affected plants are identified frequently, removed from plantations, and destroyed. In contrast, root pathogens that have wide host ranges can be difficult to manage in this way since it is usually impossible to completely remove these host parts when preparing a site for planting. *Armillaria mellea*, *Ganoderma* spp., *Rigidoporus lignosus* and *Rosellinia* spp. are notorious examples.

Different biocidal measures can be used to eliminate pathogens from soil. Their impacts range from nonspecific to somewhat specific and, due to their expense, are used only for high value crops. Flooding and broad-spectrum fumigants, such as methyl bromide + chloropicrin, eliminate large portions of the soil biota. This can be a serious problem when the targeted pathogen has saprophytic capabilities. For example, formae speciales of *Fusarium oxysporum* rapidly recolonize treated soils since they are facultative saprophytes. Other treatments such as steam and solarization have less dramatic effects and usually eliminate only temperature sensitive organisms. Most plant pathogens are killed at the 60 to 70 C that is generated by steam or the recurring more moderate temperatures, 45 to 55 C, that are generated in solarized soils. In general, fumigation, solarization, steam and chemical drenches affect only the surface horizons of soil. This can be a significant problem with pathogens that survive at lower depths.

6.5. Protection

Diverse chemical, physical and biological measures can be used to protect tropical perennial hosts from diseases. Ultimately, these are all rate-limiting measures.

Protectant fungicides are among the most common disease-management tools in agriculture. In tropical perennials, they are used at all stages of production and are key in the management of foliar and fruit diseases; without them, many high-value commodities could not be produced (Figure 14). Those that are highly susceptible to damaging diseases are prominent examples and include banana (primarily Sigatoka leafspots), citrus (several fruit and foliar diseases) and mango (primarily anthracnose).

Figure 14. Aerial application of fungicides in a banana plantation. Exported bananas of the Cavendish subgroup could not be produced in the humid tropics without the liberal and frequent use of fungicides to manage diseases, primarily the Sigatoka leaf spots (all caused by *Mycosphaerella* spp.). Photo courtesy of R.H. Stover.

Vector control can be used to indirectly protect the host from the pathogen, but there are caveats. Pesticide applications may not be cost effective unless the crop is valuable, the treatments are highly effective, and region-wide programs are utilized. For example, management of citrus greening in South Africa relies on the treatment of large areas for the psyllid vector. And when these conditions are met, additional measures may be needed, such as the use of pathogen-free planting stock and the removal of alternative weed hosts of a pathogen. For diseases in which a single feeding event by the vector is sufficient to infect the host, effective host protection is impossible. Papaya ringspot, which is caused by *Papaya ringspot virus* and vectored by transitory populations of aphids is one such disease. Vectors that reside in protected locations can be difficult to control. Examples include the phytophagous mango bud mite, *Aceria mangiferae*, which vectors *Fusarium mangiferae* and resides under leaf bud scales, and the banana aphid, *Pentalonia nigronervosa*, which vectors *Banana bunchy top virus*, and lives at the bases of and underneath leaf sheaths. Finally, efficacious measures for controlling vectors may not be available. For example, papaya bunchy top was effectively managed with DDT, since it controlled the leafhopper vectors, *Empoasca papayae* and *E. stevensi*. Without an effective replacement for this insecticide, chemical protection against this disease is no longer possible.

Modifications of the producing environments are often useful. The density of plant cover/canopy has a pronounced effect on several diseases, although its impact varies depending upon the disease. Shade reduces the severity of black Sigatoka and Panama disease of banana, but it promotes the development of algal leafspot and pink disease. In the later cases, thinning canopies to increase air flow and orienting rows such that prevailing winds and the morning sun have the greatest opportunity to dry the canopy can be helpful.

Diverse edaphic modifications are used. Improved drainage and the use of mounds or beds can significantly reduce oomycete-induced root diseases. Soil pH impacts many soilborne diseases. Acidic reactions generally favor fusarium wilts and those caused by *Rosellinia* spp., whereas basic conditions favor diseases caused by *Phymatotrichum omnivorum*. Cultural practices may indirectly effect detrimental changes; for example, monoculture and the fertilizer that was used in Hawaiian pineapple production reduced soil pH and thereby favored *Rotylenchus reniformis*, a serious pathogen of this crop.

Host nutrition and fertilization practices can have a large impact on disease development. For example, ammoniacal nitrogen increases the severity of phytophthora root rot of citrus whereas nitrate nitrogen decreases its severity.

Physical exclusion is useful in some situations. Greenhouse production of banana in Morocco protects plants from important leaf and fruit pathogens. Likewise, bags that are used to cover banana bunches in export plantations provide physical protection from insects and mechanical damage, and assist post-harvest disease control by protecting fruit from inoculum in the field. Physical barriers, such as fences, are also used to keep inoculum out of clean fields or inside those that are affected by an important disease. In export banana production in the Americas, mats that are affected by Moko disease are routinely isolated from the rest of the plantation until they have decayed and no longer pose a threat to the rest of the plantation.

Biological disease control measures have received increased attention as the numbers of available pesticides decline, the efficacy of some pesticides decrease, and concerns increase about human and environmental safety. Biocontrol of post harvest diseases of tropical fruits has focused on those caused by fungi. The unique niches that are protected and the post harvest environmental control that is possible for many of these commodities have assisted the development of effective treatments, and commercial products exist that reduce disease to levels achieved by chemical measures. Some virus-induced diseases have also been managed biologically, primarily with strains of the causal agents with attenuated virulence. For example, a nitrous acid-induced mutant of *Papaya ringspot virus* was used to cross-protect papaya plantings in Hawaii in much the same way that mild strains of *Citrus tristeza virus* have been used to protect citrus.

6.6. Resistance

Resistance to disease can be a formidable, rate-limiting tool in disease management. Genetic resistance obtained via conventional breeding has been responsible for some of the most important advances in production agriculture during the last century.

The source and effectiveness of the genes that are used depend on whether the pathogen is a generalist (resistance to diseases they cause is usually poor) or host-specialized. As mentioned above, resistance is often available for the coevolved, host-specialized diseases in the centers of origin. Many breeding success stories result from the use of such resistance.

Although useful resistance may be available to some new encounter diseases, useful genes may be infrequent in the new encounter host crop. The poor resistance that exists in new encounter situations can be circumvented if resistant, coevolved hosts are sexually compatible with the new encounter host. The late Phil Rowe’s success in breeding disease-resistant banana hybrids relied on incorporating genes from disparate taxonomic backgrounds into hybrid diploids that were then used as pollen parents.

The need for and usefulness of resistant perennial crops in the tropics should consider the type of disease that is addressed. For example, they may be critical for foliar diseases that progress rapidly (high r), but susceptible genotypes may be used for years before they need to be replaced if a slow-developing soilborne disease is involved.

Genetic resistance obtained via conventional breeding is often classified as vertical (usually controlled by one or a few major genes) or horizontal (several genes). Much has been written about the dangers of vertical resistance. Although high levels of resistance can be achieved with it, it is usually pathotype specific and can be easily overcome by the evolution or selection of virulent pathotypes. Thus, its use in perennial crops can be dangerous.

The phenomenon of initial, excellent disease control that eventually erodes in vertically resistant hosts has been called the “boom-and-bust” cycle. It is most common with foliar diseases that have the potential for rapid epidemic development and are caused by pathogens with a high evolutionary potential; i.e., those that are genetically variable and have both sexual and asexual life cycles. Although vertical resistance is usually not durable, it can be useful in some situations. For valuable crops in which good production (the "boom" part of the cycle) can be very profitable, long-term resistance may not be necessary. Acceptable production may be possible during the time that is needed to develop new resistant germplasm to combat the eventual, resistance-breaking pathotypes, especially when the pathogen has a low evolutionary potential.

Genetic transformation for disease resistance (the creation of Genetically Modified Organisms, GMOs) can be quite effective. Virus-induced diseases have lent themselves to this approach far more often than diseases caused by other pathogen groups, and there are some notable success stories. For example, the papaya industry in Hawaii was saved by selections that were genetically engineered for resistance to *Papaya ringspot virus*. In general, conventional materials are more accepted in the marketplace than are GMOs, especially in Europe. As consumers become better educated about the benefits and safety of GMOs, a greater acceptance of these products may occur.

6.7. Treatment of Diseased Plants

Diseased plants can be treated effectively with various curative (systemic) chemicals. These are rate-limiting measures.

Although systemic pesticides can be very effective, their specific modes of action often make them susceptible to the development of resistance. In general, rare variants of the pathogen can be selected by the continued use of these chemicals. As they predominate, the compound loses effectiveness. The propensity of different pathosystems and classes of pesticides to lose effectiveness over time can be evaluated in much the same way that the durability of host resistance is analyzed (see above). For example, the *M. fijiensis*:banana pathosystem can be classified as high risk since the pathogen has a short generation time, sporulates abundantly, and has a sexual cycle that facilitates the development of resistance. Among the systemics that have been used against black Sigatoka, the benzimadizoles are ranked as high risk, since resistance to them develops rapidly, whereas the strobilurins fungicides are at moderate risk.

Two systemic pesticides, metalaxyl and fosetyl-Al (and its phosphonate derivatives) are effective against oomycetes. Although metalaxyl is effective against a wider range of species than the phosphonates, it is more prone to the development of resistance and can also be microbially degraded in the soil, resulting in a rapid loss of activity. Fosetyl-Al and its active metabolite phosphorous acid are phloem, as well as xylem, mobile. This mobility enables effective concentrations of phosphonate metabolites to be translocated to above- and below-ground portions of plants when these compounds are applied as soil drenches or sprayed on foliage. When insufficient leaves or roots in diseased plants exist for their uptake, trunk injection is an effective means of application. Phytophthora root rot of avocado and *P. palmivora*-induced diseases of other tropical perennials are among the diseases that are managed effectively in the later manner.

7. Conclusions

Diverse pathogens cause diseases of tropical fruit crops. They can be limiting factors in the production and marketing of these commodities, and are often difficult to damage.

They are scientifically interesting problems. New vectors, as for mango malformation, or pathogens, as for bunchy top of papaya, are associated with some of the diseases. And some are caused by two or more distinct taxa; for example, citrus greening, mango malformation and fusarium wilt of banana.

Some of the most important tropical fruit diseases are host-specific and are caused either by coevolved or new-encounter pathogens. Resistance, the most effective tool with which many of these diseases are managed, is usually available in coevolved pathosystems but may be uncommon in new encounter situations. Inadequate host resistance can be a significant barrier in the management of new encounter diseases, as well as those that are caused by generalist pathogens. In the later cases, other disease management tactics are needed.

Glossary

Anamorph: The asexual state of a fungus; known formerly as the "imperfect" state.

Disease: A condition whereby the natural function of a host is disturbed or harmed by ongoing insult from a pathogen. Pathogens are usually biotic and infectious. Exceptions include viruses and viroids, that can be considered abiotic agents since they do not respire, and noninfectious biotic pathogens that cause disease without colonizing the host.

Epidemiology: The study of epidemics, episodes of disease, in time and space.

Teleomorph: The sexual state of a fungus; known formerly as the "perfect" state. Life stage during which nuclear fusion followed by meiosis occurs.

Vector: An organism that moves a pathogen to an infection court on a host. For plant-pathogenic viruses, mollicutes and proteobacteria, vectors are most often fungi, insects, mites and nematodes.

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Biographical Sketch

Randy C. Ploetz graduated from Purdue University in 1974 with a B.Sc. in Forestry and in 1976 with a M.Sc. in Plant Pathology. In 1984, he received a Ph.D. in Plant Pathology from the University of Florida, and in 1986 joined the faculty at the university's Tropical Research and Education Center. He was promoted to professor in 1996, and received the University of Florida Research Foundation Professor Award in 2004 and the International Service Award of the American Phytopathological Society in 2008. Randy was Editor-in-Chief of APS Press from 2000 to 2002, a Senior Editor on that editorial board from 1995 to 2000, and an Associate Editor for *Phytopathology* from 1995 to 1997. He is a former President of the Florida Phytopathological Society and former Vice-President and managing Editor for refereed papers for the Florida State Horticultural Society. He has written over 300 publications on tropical fruit diseases, edited/written four books, and is writing a two-volume book for Springer-Verlag, *Tropical Plant Pathology*.