

Diseases of Tropical Perennial Crops: Challenging Problems in Diverse Environments

The world's oldest ecosystems are found in the tropics. They are diverse, highly evolved, but barely understood. Diseases that impact crops in these regions can be significant constraints to production, especially when they occur in lowland environments with high rainfall and uniform, warm temperatures; respites from disease pressure there are often infrequent. Difficulties in managing diseases in the humid tropics are multiplied when the affected crops are perennial. The favorable conditions for disease development and the presence of susceptible host tissue over long periods make diseases of tropical perennial crops serious management challenges.

This topic is introduced with a few concepts on the occurrence and development of these pathosystems. Peculiar aspects and scenarios that influence the types of and extent to which different diseases develop are summarized. Measures that are useful on annual or short-term crops may be ineffective against these diseases. 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 of the diseases are caused by two or more distinct taxa; for example, citrus greening, mango malformation, Panama disease, and tracheomycosis of coffee. Some of the most important diseases are host-specific and are caused by either 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 both coevolved and new encounter diseases.

General tactics are described that are useful against diseases of tropical perennials. 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. All of these approaches are discussed with tropical perennial examples.

Agriculture Begins

Agriculture began after the Pleistocene (last ice age) and started independently in several different regions (Table 1). It developed first in the Near East (sites in the Fertile Crescent and in present-day Israel and Turkey) due to a fortuitous combination of suitable climate and useful plants and animals that could be domesticated (33,76,144). These first farmers appeared at least 11,000 years ago, and were followed in quick succession by others in Northern and Southern China, Mesoamerica, New Guinea, the Andes, and the Eastern United States (32–34). Additional areas of independent development may also include Amazonia, Ethiopia, the Sahel, Southeast Asia, and Western Africa.

During agriculture's brief history, humans have utilized numerous plants (12,21,91,135,148). At least 3,000 taxa have been used for food and several hundred more have been used for other purposes. In Table 2, the following categories have been considered: beverage, drug, elastomer, fiber, food, insecticide, oil, spice, and timber and pulp.

Despite the large numbers of useful species, only a subset is very significant and few are of major importance (114,128,136, 143,148). Scarcely more than a hundred species enter world commerce, and among the food crops, few are staples: About 0.5% of the food species supply more than 90% of the world's food (42,148).

Biological Diversity in the Tropics

Biological diversity increases with decreasing latitude (61,67,162). This trend, called the Latitudinal Diversity Gradient (LDG), has been observed for a wide range of trophic levels and life forms. In general, species numbers increase dramatically as one moves from the poles to the equator.

The LDG is one of the oldest recognized patterns in the biological sciences. Hum-

boldt (63) discussed the relationship two centuries ago, and Darwin (26) wrote about it in his famous book. This increase in diversity is most pronounced in tropical rain forests, which are thought to host 50% of all species but occupy only 7% of the world's landmass (162). And it appears to be a general rule on our planet since it is found in the fossil record and re-establishes after mass extinctions (67).

Plants are among the most prominent organisms that conform to the LDG. Thus, it is not surprising that most of the early agricultural hubs (nine of the above 12) and first crop domestications occurred in the tropics, i.e., between the Tropics of Cancer and Capricorn (Table 1). More than half the crops in Table 2, 69 of 126 (55%), originated in the tropics. Some tropical annuals, e.g., rice, potato, and maize, are now also grown in temperate zones during the summer. But essentially all tropical perennials are restricted to the tropics due to their cold sensitivity.

A wide range of habitats is found in the tropics, including humid lowlands, deserts, seasonally dry forests, grasslands, savannahs, montane environments, and swamps (148,161). Further diversity in each of these habitats results from variable edaphic, meteorologic, and biotic conditions. This vast array of environments enables an equally wide range of plants to be grown; almost every crop in Table 2 can be grown somewhere in the tropical world. For example, important temperate domesticates are grown in the lowland tropics (members of the Brassicaceae and Fabaceae are especially common) and at high elevations where moderate temperatures exist (members of the Fabaceae, Poaceae, and Rosaceae are most notable) (114). Thurston's (148) estimate that twice as many crops are grown in the tropics as in the temperate zones of the world is probably accurate.

Studies that compare tropical and temperate ecosystems are uncommon, and a disproportionate amount of the research on microorganisms has been conducted in temperate zones. For example, in reviewing the literature on fungi and bacteria in forest ecosystems since 1963, Lodge et al. (87) found only 96 references for tropical forests, but 2,411 for temperate forests. Despite this disparity, the LDG is also evident among microbes.

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Three groups of nonpathogenic fungi, decomposers (86), endophytes (6), and arbuscular mycorrhizae (64), are very diverse in the tropics, as are fungi in general (156,157). Plant pathogens also appear to be more numerous and diverse in the tropics. One group, the flagellated protozoa (*Phytomonas* spp.), is rare outside the tropics (2), and 60% of the described viroid species have tropical, natural hosts (55).

If one considers diseases of crop plants, there may be an even greater difference between temperate and tropical areas. Wellman (161) found a pronounced temperate/tropical bias among the crops that were well represented in both zones: pumpkin and squash, 19 temperate diseases and 111 tropical; sweet potato, 15/187; tomato, 32/278; common bean, 52/253+; and potato, 91/175. Wellman (159–161) concluded that for every disease that occurred on a given crop in temperate areas there were 10 in the tropics.

Disease problems can be severe in the tropics, especially where high rainfall and uniform, warm temperatures are the norm. These conditions are highly favorable for the development of most diseases, and respites from disease pressure are usually infrequent in these areas. Overall, losses are thought to be 50 to 100% higher in tropical than in temperate regions (60,148). Estimates of the proportion of all losses in the tropics that are caused by diseases range from 30% (56) to 50% (161).

Plant pathology began in, and generally continues to be a discipline focused on,

temperate climates; comparatively little plant pathological research has been conducted in the developing tropical world (143). Work in the tropics has made significant contributions to the discipline of plant pathology (100,132), but much more would be revealed if resources that approached those used in temperate zones were devoted to research in the tropics.

Perennial crops: Challenging hosts for disease managers. When one considers the total areas planted and annual yields, the most important food crops are annuals. Other than sugarcane (its total represents harvested cane, not a final product), only production figures for maize, rice, and wheat exceed 500 million metric tons per year (Table 2). Although they are minor components of most natural floras, annuals predominate in agriculture for the following reasons: they produce quick results after planting; when stored, they enable escape from unfavorable climatic conditions (particularly the grains and pulses); and when incorporated in fallow or rotation cultures, they facilitate the avoidance of pests and pathogens (128).

Despite the importance of annual crops, Table 2 indicates that perennial crop plants (those that live longer than 2 years [4]) are more numerous (73 of the 126 [58%]). There are several reasons why these most common hosts are often serious disease management challenges.

Rather than being protected for a few weeks or months, perennial hosts require long-term measures. Since they are long-lived and there are no seasonal breaks in production, perennials are more prone to

inoculum buildup and epidemic disease development.

Managing the large reservoirs of inoculum and high disease pressures that develop in perennial monocultures can be difficult and costly. For example, management of black Sigatoka leaf spot of banana (black leaf streak), caused by *Mycosphaella fijiensis*, contributes as much as 25% of the final retail cost of export bananas and can fail during periods of high rainfall or less than adequate fungicide applications (105). In India, 10% of the total costs of coffee production went toward the control of rust (130). And eradication efforts can be very expensive. Cacao swollen shoot, caused by *Cacao swollen shoot virus*, in West Africa and citrus canker, caused by *Xanthomonas axonopodis* pv. *citri*, in Florida are worst-case examples of where large sums of money were invested in ultimately unsuccessful campaigns.

Due to long-term selection pressure, there are increased opportunities in perennial systems for the development of pesticide-resistant pathogens. Despite an increased awareness of pesticide resistance and the establishment of strategies to avoid the build-up of resistant strains (11), a rapid erosion of the efficacy of new chemicals is still common (68,120).

Long-term exposure to disease-promoting or predisposing factors can increase disease development in perennial hosts (7). Host nutritional status is an important abiotic factor that can be related to increased disease (27,101). Likewise, an excess of water can encourage the development of diseases induced by stramenopiles

Table 1. Crop plants that were domesticated in early agricultural centers^z

Area	First dates (years B.P.)	Crops					
		Grasses and grains	Pulses	Fiber	Root and tubers	Melons and squash	Fruit and vegetables
Fertile Crescent	11,500	Emmer and einkorn wheat, barley	Pea, lentil, chickpea	Flax	None	Muskmelon	Date, fig
China	10,000	Rice, foxtail and broomcorn millet	Soybean, adzuki bean, mung bean	Hemp	None	None	None
MesoAmerica	10,000	Maize	Common bean, tepary bean, scarlet runner bean	Cotton (<i>G. hirsutum</i>), <i>Yucca</i> spp., <i>Agave</i> spp.	Jicama	Squashes (<i>C. pepo</i> , etc.)	Pepper (<i>Capsicum</i> spp.), avocado
Andes, Amazonia	3,500-1,000	Quinoa	Lima bean, common bean, peanut	Cotton (<i>G. barbadense</i>)	Cassava, sweet potato, potato, oca	Squashes (<i>C. maxima</i> , etc.)	Pineapple
West Africa and Sahel	3,000 and 5,000	Sorghum, pearl millet, African rice	Cowpea, groundnut	Cotton (<i>G. herbaceum</i>)	Yams	White-flowered (bottle) gourd	Watermelon
India	5,000	None	Hyacinth bean, black gram, green gram	Cotton (<i>G. arboreum</i>), flax	None	Cucumber	Mango
Ethiopia	3,000	Teff, finger millet	None	None	None	None	None
Eastern USA	2,500-1,000	Maygrass little barley, knotweed, goosefoot	None	None	Jerusalem artichoke	Squash (<i>C. pepo</i>)	None
New Guinea	7,000	Sugarcane	None	None	None	None	Banana

^z Adapted from refs. 33 and 136; additional data are from 32, 34, 76, and 128.

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

	Order	Family (subfamily)	Crop(s), taxa	Category/usage	Center of origin ^v	Major production areas	Production, 2005 (t)		
Gymnosperms	Coniferales	Pinaceae	Pines, <i>Pinus</i> spp.	Timber, pulp	Diverse Northern Hemisphere	Temperate to tropical	N.A.		
			Spruces, <i>Picea</i> spp.	Timber, pulp					
			Larches, <i>Larix</i> spp.	Timber, pulp				Temperate	N.A.
			Douglas firs, <i>Pseudotsuga</i> spp.	Timber, pulp				Temperate	N.A.
Angiosperms			Spruces, <i>Picea</i> spp.	Timber, pulp	Northern Hemisphere	Temperate	N.A.		
Magnoliid complex	Laurales	Myristicaceae	Nutmeg, mace, <i>Myristica fragrans</i>	Spice	Moluccas	Indonesia, Grenada, Sri Lanka, India, Malaysia	81,292		
		Lauraceae	Avocado, <i>Persea americana</i>	Fruit	Tropical America	Mexico, USA, Indonesia, South Africa, Chile	3,229,134		
			Cinnamon, <i>Cinnamomum verum</i> ^w	Spice	Sri Lanka	Indonesia, Sri Lanka, India, Seychelles, Madagascar	134,410		
	Piperales	Piperaceae	Black pepper, <i>Piper nigrum</i>	Spice	Southwest India	India, Indonesia, Brazil	411,359		
Monocots	Alistamatales	Araceae	Taro, <i>Colocasia esculenta</i>	Root and tuber	Indo-Malaya	West Africa, Pacific	10,586,651		
			Yautia (tanier), <i>Xanthosoma sagittifolium</i>	Root and tuber	Tropical America	Caribbean, West Africa, Pacific	421,966		
	Asparagales	Orchidaceae	Vanilla, <i>Vanilla planifolia</i>	Spice	SE Mexico, C. America	Madagascar, Indonesia, China	10,539		
		Alliaceae	Garlic, onion, <i>Allium</i> spp.	Spice	Near East	USA, Japan, Spain	14,548,669		
		Agavaceae	Agave fibers, <i>Agave</i> spp. (mainly sisal, <i>A. sisalana</i>)	Fiber	MesoAmerica, Caribbean	Brazil, East Africa	385,463		
	Dioscoreales	Asparagaceae	Asparagus	Vegetable			6,658,007		
		Dioscoreaceae	Yams, <i>Dioscorea</i> spp.	Root and tuber	Asia, Africa, Tropical America	West Africa, Southeast Asia, Oceania, Caribbean	39,856,954		
	Arecales	Arecaceae (Palmae)	Betel nut, <i>Areca catechu</i>	Drug-medicinal	Southeast Asia	Southeast Asia	727,425		
			Coconut, <i>Cocos nucifera</i>	Fruit, oil, fiber (coir)	Southeast Asia	Philippines, Indonesia, India, Sri Lanka	55,234,124 (fruit), 954,290 (coir)		
			Oil palm, <i>Elaeis guineensis</i> ^x	Oil	West Africa	Indonesia, Malaysia	173,391,199 (fruit)		
			Date, <i>Phoenix dactylifera</i>	Fruit	N. Africa, Middle East	Iraq, Iran, Egypt	6,921,950		
	Poales	Bromilaceae	Pineapple, <i>Ananas comosus</i>	Fruit	South America	Thailand, Philippines, Brazil	16,769,660		
		Poaceae (Bambusoideae)	Bamboos, many genera	Timber, fiber	Mostly tropical	Mostly tropical	N.A.		
		Poaceae (Ehrhartoideae)	Rice, <i>Oryza sativa</i>	Grain	IndoChina	Global	618,440,644		
Poaceae (Pooideae)		Oats, <i>Avena</i> spp.	Grain	Europe	Temperate world	23,953,749			
		Barley, <i>Hordeum vulgare</i>	Grain	Southwest Asia	Europe, N. Africa, Near East, Russia, China, India, Canada, USA	139,043,947			
		Rye, <i>Secale cereale</i>	Grain	Southwestern Asia	Europe, Russia	15,515,206			
		Wheats, mainly <i>Triticum aestivum</i>	Grain	Fertile Crescent	Global	629,566,0417			

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^u Listed taxa chosen based on importance described elsewhere (42,135,136). Taxa are listed based on their phylogenetic relatedness (adapted from Stevens [139]).

^v Center of origin based on best available evidence. Questionable or unclear centers are denoted with a ?.

^w At least 10 species of *Cinnamomum* are sold in the spice trade, notably the cassias, but only *C. verum* is considered true cinnamon (158).

^x An American species, *E. oliefera*, has been used to produce disease-resistant interspecific hybrids.

^y Includes plantains, as well as dessert and cooking bananas.

^z Due to its transcontinental spread via floating seed, kapok has long been a pantropical crop.

Table 2. (Continued from previous page)

Order	Family (subfamily)	Crop(s), taxa	Category/usage	Center of origin ^v	Major production areas	Production, 2005 (t)		
Eudicots (tricolpates)	Poaceae (Panicoideae)	Sugarcane, <i>Saccharum</i> spp.	Sugar	New Guinea	India, Cuba, Brazil	1,291,685,924		
		Millets, <i>Eleusine coracana</i> , <i>Pennisetum americanum</i>	Grain	Africa		28,559,553		
		Sorghum, <i>Sorghum bicolor</i>	Grain	Africa	Global	58,668,212		
		Maize, <i>Zea mays</i>	Grain	Mexico, C. America	Global	710,675,149 (dry + green)		
	Zingiberales	Musaceae	Banana ² , <i>Musa</i> spp.	Fruit	Southeast Asia	Tropical America, Africa	105,815,354	
			Abacá (Manila hemp), <i>Musa textilis</i>	Fiber	Philippines	Philippines, Central America	100,987	
			Ginger, <i>Zingiber officinale</i>	Spice	Southeast Asia	India, Southeast Asia	1,004,546	
	Caryophyllales	Amaranthaceae	Amaranth, <i>Amaranthus</i> spp.	Grain	Subtrop., trop. America	Asia	N.A.	
			Quinoa, <i>Chenopodium quinoa</i>	Grain	Andes	Andes	57,765	
			Sugar beet, <i>Chenopodium vulgare</i>	Sugar	Europe	Europe, Russia, USA	240,984,299	
			Spinach, <i>Spinacia oleracea</i>	Vegetable	SW Asia	Europe, Americas	12,980,944	
			Buckwheat, <i>Fagopyrum</i> spp.	grain	Temperate E. Asia	Russia, France, USA, Canada	2,649,524	
		Polygonales	Polygonaceae					
			Grossulariaceae	Gooseberry, <i>Ribes</i> spp.	Fruit	Europe, N. America		134,452
		Vitales	Vitaceae	Currant, <i>Ribes</i> spp.	Fruit	Europe		862,232
				Grapes, mainly <i>Vitis vinifera</i>	Fruit	C. Asia	Mediterranean Europe, USA	65,584,122
		Malpighiales	Euphorbiaceae	Tung, <i>Aleurites</i> spp.	Oil	East Asia	China, Argentina, USA, Brazil	517,480
	(Para) rubber, <i>Hevea brasiliensis</i>			Elastomer	Amazon	Indonesia, Malaysia	9,123,590	
			Cassava, <i>Manihot esculenta</i>	Root and tuber	South America	South America, Africa	203,061,895	
			Castor (bean), <i>Ricinus communis</i>	Oil	Africa?	Brazil, India, Russia, China	1,393,812	
Linaceae	Flax, linseed, <i>Linum usitatissimum</i>		Fiber, oil	Eurasia	Temperate world	887,227 (fiber), 693,000 (seed)		
	Passifloraceae		Passionfruit, <i>Passiflora</i> spp.	Fruit	Tropical America	Tropical America	1,000,000	
Fabales	Salicaceae		Aspens and poplars, <i>Populus</i> spp.,	Timber, pulp	Temperate to arctic north	Temperate to arctic north	N.A.	
	Fabaceae (Papilionoideae)		Peanut (groundnut), <i>Arachis hypogaea</i>	Pulse, oil	Argentina, Bolivia		35,865,389	
			Pigeon pea, <i>Cajanus cajan</i>	Pulse	India	India	3,476,995	
			Chickpea, <i>Cicer arietinum</i>	Pulse	Western Asia	India, Mediterranean	8,694,192	
		Soybean, <i>Glycine max</i>	Oil, pulse, forage	Northeast Asia	USA, South America	214,347,289		
		Lentil, <i>Lens culinaris</i>	Pulse	Near East	India, Pakistan, Ethiopia, Near East, Mediterranean	4,059,587		
		Alfalfa (lucerne), <i>Medicago sativa</i>	Forage	Iran	N. America, Europe, S. America	N.A.		
		Lima bean, <i>Phaseolus lunatus</i>	Pulse	Middle, S. America	Subtropics, tropics	N.A.		
		Common bean, <i>Phaseolus vulgaris</i>	Pulse	Middle, S. America	Global	25,160,509 (dry + green)		
		Pea, <i>Pisum sativum</i>	Pulse	Near East?	N. Europe, Russia, China, NW USA	20,283,678 (dry + green)		
Clovers, <i>Trifolium</i> spp.		Forage	Eastern Mediterranean	Temperate world	N.A.			
Broad (field) bean, <i>Vicia faba</i>	Pulse	Europe, Near East	N. temperate world	5,778,600 (dry + green)				

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Table 2. (Continued from previous page)

Order	Family (subfamily)	Crop(s), taxa	Category/usage	Center of origin ^v	Major production areas	Production, 2005 (t)			
Rosales	Rosaceae	Cowpea, <i>Vigna unguiculata</i>	Pulse	Ethiopia?	India, W. Africa.	3,766,540 (dry)			
		Bambara groundnut, <i>Voandzeia subterranea</i>	Pulse	Tropical Africa		61,500			
		Strawberry, <i>Fragaria ananassa</i>	Fruit	Europe	Europe, Russia, USA	3,616,865			
		Apples, <i>Malus</i> spp.	Fruit	Asia Minor, Caucasus, C. Asia	Temperate world	59,444,377			
		Almond, <i>Prunus amygdalus</i>	Nut	Central - Western Asia	Temperate world	1,648,916			
		Apricot, <i>Prunus armeniaca</i>	Fruit	W. China	Temperate world	2,820,659			
		Cherry, <i>Prunus</i>	Fruit	C. Asia	Temperate world	3,008,390 (sweet + sour)			
		Peach and nectarine, <i>Prunus</i>	Fruit	W. China	Temperate world	15,782,002			
		Plum, <i>Prunus</i> spp.	Fruit	N. America, Europe	Temperate world	9,458,503			
		Pears, <i>Pyrus</i> spp.	Fruit	E. Asia	Temperate world	19,539,311			
		Quinces, <i>Cydonia</i>	Fruit			387,540			
		Raspberries, blackberries, <i>Rubus</i> spp.	Fruit	Europe, USA	Europe, USA	498,102			
			Cannabidaceae	Hemp, <i>Cannabis sativa</i>	Fiber, drug-medicinal, oil	Temperate Asia	Russia, India	67,460 (fiber), 32,160 (seed)	
			Moraceae	Breadfruit, <i>Artocarpus</i> spp.	vegetable	Polynesia	Polynesia	N.A.	
				Fig, <i>Ficus carica</i>	Fruit	Southern Arabia	Turkey, Egypt, Greece, Iran, Morocco	1,075,174	
Cucurbitales	Cucurbitaceae	Hops, <i>Humulus lupulus</i>		Europe	Europe, temperate world	100,976			
		Ramie, <i>Boehmeria nivea</i>	Fiber	Malaysia, China, Japan	China	249,500			
		Watermelon, <i>Citrullus lanatus</i>	Fruit	Southern Africa		96,455,182			
		Cucumber, <i>Cucumis sativus</i>	Vegetable	India		41,836,847			
		Cantaloupe (muskmelon), <i>Cucumis melo</i>	Fruit	Africa		28,349,422			
		Squashes, pumpkins, gourds, <i>Cucurbita</i> spp.	Vegetable	Tropical America		19,816,731			
		White-flowered (bottle) gourd <i>Lagenaria siceraria</i>	Vegetable	Southern Africa		N.A.			
			Fagales	Fagaceae	Chestnut, <i>Castanea</i> spp.	Nut	Northern temperate	1,124,999	
				Juglandaceae	Walnuts, <i>Juglans</i> spp.	Nut	Europe, N. America	China, Europe, N. America	1,526,816
				Betulaceae	Hazelnuts (filberts), <i>Corylus</i> spp.	Nut	Europe, SW Asia	705,219	
Myrtales	Myrtaceae	Allspice, <i>Pimenta dioica</i>	Spice	Caribbean basin		2,481,241			
		Clove, <i>Syzygium caryophyllus</i>	Spice	Moluccas	Zanzibar, Pemba, Madagascar, Indonesia	145,370 (whole + stems)			
						N.A.			
Brassicales	Caricaceae	Eucalyptus, <i>Eucalyptus</i> spp.	Timber	Australia		N.A.			
		Papaya, <i>Carica papaya</i>	Fruit	Central America	Brazil, Nigeria, India, Mexico, Indonesia	6,810,727			
	Brassicaceae	Turnip, <i>Brassica campestris</i>	Vegetable	Mediterranean, Afghanistan, Pakistan		N.A.			

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Table 2. (Continued from previous page)

Order	Family (subfamily)	Crop(s), taxa	Category/usage	Center of origin ^v	Major production areas	Production, 2005 (t)
Malvales	Malvaceae (Malvoideae)	Cabbages, kales, cauliflower, broccoli, <i>Brassica oleracea</i>	Vegetable	Mediterranean, Asia Minor		86,200,900
		Swedes, rapes, <i>Brassica napus</i>	Vegetable	Europe-Mediterranea		N.A.
		Mustards, <i>Brassica</i> spp., <i>Sinapis alba</i>	Vegetable			623,253 (seed)
		Radish, <i>Raphanus sativus</i>	Vegetable	Mideast-Mediterranean?		N.A.
		Okra, <i>Abelmoschus esculentus</i>	Vegetable	W. Africa (Ethiopia?)	Subtropics, tropics	5,041,694
		Cottons, <i>Gossypium</i> spp.	Fiber, oil	Mostly tropics	Global	18,586,467 (lint), 33,442,393 (cottonseed)
		Kapok, <i>Ceiba pentandra</i>	Fiber	Tropical America ^z	Southeast Asia	122,000 (fiber), 392,967 (fruit), 331,296 (seed in shell)
		Kola(nut), <i>Cola nitida</i>	Drug-medicinal	W. Africa	W. Africa	221,000
		Jute, <i>Corchorus</i> spp.	Fiber	India	India	3,250,322
		Cacao, <i>Theobroma cacao</i>	Confectionary, beverage	South America	West Africa	3,822,009 (beans)
Sapindales	Dipterocarpaceae	Dipterocarps, <i>Shorea</i> spp., <i>Hopea</i> spp., <i>Dipterocarpus</i> spp., <i>Vatica</i> spp.	Timber	Southeast Asia	Southeast Asia	N.A.
		Citrus, <i>Citrus</i> spp.	Fruit	Southeast Asia	USA, Brazil	105,440,168
		Mahoganies, <i>Swietenia</i> spp., <i>Khaya</i> spp.	Timber	Tropics	Tropics	N.A.
		Cashew, <i>Anacardium occidentale</i>	Fruit, nut	Tropical America	Tropical America	1,718,010 (cashewapple) 2,337,358 (cashew nut)
		Mango, <i>Mangifera indica</i>	Fruit	India, Southeast Asia	India, China, Mexico, Thailand, Pakistan	28,221,510
		Pistachio, <i>Pistacia vera</i>	Nut	C. Asia	Near East	489,209
		Karite (shea) nut, <i>Butyrospermum paradoxum</i>	Oil	W. Africa	W. Africa	693,000
		Kiwifruit (Chinese gooseberry), <i>Actinidia deliciosa</i>	Fruit	S. China	New Zealand, Chile	1,120,938
		Persimmon, <i>Diospyros kaki</i>	Fruit	Asia	Asia, N. America, S. Europe	2,561,732
		Tea, <i>Camellia sinensis</i>	Beverage	China	China, India	3,436,180
Ericales	Lecythidaceae	Brazilnut, <i>Bertholletia excelsa</i>	Nut	Northern S. America	Bolivia, Brazil	73,960
		Blueberry, cranberry, <i>Vaccinium</i> spp.	Fruit	N., S. America, Europe		242,610 386,160
		Sweet potato, <i>Ipomea batatas</i>	Root and tuber	Tropical America	Subtropics, tropics	129,392,309
		Pepper, chile, <i>Capsicum</i> spp.	Vegetable, spice	Tropical America	Temperate, tropical world	24,941,587
		Tomato, <i>Lycopersicon esculentum</i>	Vegetable	Tropical America	Global	122,659,873
		Tobacco, <i>Nicotiana tabacum</i>	Drug-medicinal	Tropical America	Global	6,564,017
		Eggplant (aubergine), <i>Solanum melongena</i>	Vegetable	India?	Subtropics, tropics	30,477,775
		Potato, <i>Solanum tuberosum</i>	Root and tuber	Tropical America	Global	323,102,918

(continued on next page)

Table 2. (Continued from previous page)

Order	Family (subfamily)	Crop(s), taxa	Category/usage	Center of origin ^v	Major production areas	Production, 2005 (t)
Gentianales	Rubiaceae	Cinchona (quinine), <i>Cinchona</i> spp.	Drug-medicinal	Andes	Indonesia	N.A.
		Coffees, <i>Coffea arabica</i> , <i>C. canephora</i>	Beverage	Ethiopia, W. Africa	Tropical America	7,779,495 (green beans)
Lamiales	Oleaceae	Olive, <i>Olea europaea</i>	Oil	Mediterranean	Spain, Italy, Greece	14,442,435 N.A.
	Lamiaceae	Teak, <i>Tectona grandis</i>	Timber			
	Pedaliaceae	Sesame, <i>Sesamum indicum</i>	Oil	Africa?	India, China, Sudan, Mexico, Venezuela, Burma	3,325,679
Apiales	Apiaceae	Carrot, <i>Daucus carota</i>	Vegetable	Afganistan	Temperate world	24,481,021
Asterales	Asteraceae	Safflower, <i>Carthamus tinctorius</i>	Oil	Near East	India, USA, Mexico	805,667
		Pyrethrum, <i>Chrysanthemum</i> spp.	Insecticidal	Caucasus, NW Persia		13,405 (dry flowers)
		Sunflower, <i>Helianthus annuus</i>	Oil	Midwestern USA	Russia, Argentina, Balkans	30,944,162
		(Globe) artichoke, <i>Cynara cardunculus</i>	Vegetable	Mediterranean, Canary Islands	Europe, USA	1,203,775
		Lettuce, <i>Lactuca</i> spp.	Vegetable	Eastern Mediterranean	N. America, Australia, Europe, S. America	22,204,280

and bacteria, whereas water deficits can predispose crops to other diseases (39,101,107). Insect damage and other diseases are among the biotic factors that affect host susceptibility (101,131,147). For example, canker 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 the Diaprepes root weevil, *Diaprepes abbreviatus* (150), whereas the development of anthracnose of avocado, caused by *Colletotrichum gloeosporioides*, is increased by scab damage, caused by *Sphaceloma perseae* (95).

In perennial systems, there are increased opportunities for pathogen movement within and among plantations. This occurs with all contagious diseases, but can be especially important with slow-moving diseases that might retain a restricted distribution in a short-season crop (107,140,166). Given sufficient time, even sedentary soilborne problems can spread significantly.

When explosive aboveground diseases are involved, new strains (47) or taxa (151) that are more fit or virulent than pre-existing populations can rapidly increase to dominate a field or region. This process is most rapid when there is no seasonal opportunity to change to resistant genotypes and hosts are grown in monocultures. Diseases are usually far less damaging in intercropped production (147) and in natural ecosystems (15,17) than they are in uniform plantings. Yellow rust of coffee, *Coffea arabica*, caused by *Hemileia vastatrix*, and South American leaf blight of Para rubber, *Hevea brasiliensis*, caused by *Microcyclus ulei*, are two examples of dis-

eases that are innocuous in mixed or natural systems but become enormous problems in monocultures (40,92).

Multilines and cultivar mixtures have been used to discourage epidemic disease development in annual crops, and rusts and powdery mildews of cereals are common targets (49,98). This approach is relatively uncommon with perennials, especially when cultivar identity is required in the marketplace. There is also evidence to suggest that when hosts are large, autoinfection may negate the beneficial impact of heterogeneous host mixes (17,49,116). In a recent review, Mundt (98) mentioned only one perennial crop in the tropics, coffee, in which mixes of resistant cultivars were used to combat rust.

Replacing susceptible perennial hosts is costly, and it often takes several years before widespread changes can be made. Schieber (130) indicated that it took about 10 years for rust-susceptible coffee cultivars to be replaced; and the transition to Cavendish cultivars that resisted Panama disease, caused by *Fusarium oxysporum* f. sp. *cubense*, in the American banana trades took a decade or longer (140).

Finally, perennial crops are more apt to be affected by variable production or economic factors than annual crops. The impact of coffee rust provides examples. Avelino et al. (7) demonstrated that seasonal and site-specific variation affected the development of coffee rust and resultant yield; fungicidal management of this disease was justified only in some years and some locations. In marginal production areas where low yield potentials resulted in narrow profit margins, the use of fungicides was never justified (130). In these areas, rust-resistant cultivars were

most important (118,133). Given the dramatic fluctuations that occur in global coffee prices (1), it is reasonable to assume that fungicide applications for rust control would be reduced if market returns were low.

Diseases of Tropical Perennial Crops

The disease challenges that face producers of tropical perennial crops are outlined in the following sections. As discussed above, the overall picture is one of diverse pathogens and host plants in what are often disease-conducive environments (148,161). These are difficult problems. Due to their polycyclic nature, measures that are useful on annual or short-term crops may be ineffective. In general, more effective and durable management options are needed in perennial situations, especially when there is no winter or off-season during which inoculum and disease pressure would be reduced (see Buddenhagen [14] for a contrasting view). It is not surprising that diseases can be serious constraints in the production of tropical perennials, and that special strategies may be needed to effect their management.

Below, some basic concepts are presented on the occurrence and development of these pathosystems. Peculiar aspects of these diseases and scenarios that influence the types and the extent to which they develop are summarized. They are scientifically interesting problems. New vectors (mango malformation) or pathogens (bunchy top of papaya) are associated with some of these diseases, and several are caused by two or more taxa, for example, bud rot of betel nut and coconut, citrus greening, mango malformation, Panama disease, phytoplasma diseases of coconut,

and tracheomyces of coffee (29,58,89, 107, 109,117,123,150; C. S. Lima, L. H. Pfenning, S. S. Costa, M. A. Campos, and J. F. Leslie, *unpublished*). Some of the most important diseases are host-specific or have restricted host ranges; they are caused by either 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 is uncommon in some new-encounter situations. Inadequate host resistance represents a significant barrier to managing many new-encounter diseases.

This review concludes with general tactics that are useful against diseases of tropical perennials. The successful management of plant disease utilizes several principles and practices, regardless of the host and the environment in which it is grown (101,143,154,165). 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. All of these approaches are discussed with tropical perennial examples.

Coevolved pathosystems. Although the term “coevolution” was first coined in 1964 to describe butterfly:plant interactions (38), the idea that tandem evolution occurs between species was discussed by Darwin (26) and described in the 1950s in a plant-pathological context (20). In describing results from his classic research on flax rust, Flor (46) suggested that “...obligate parasites, such as the rust fungi, must have evolved in association with their hosts” and that “...during their parallel evolution, host and parasite developed complementary genic systems.” Gene-for-gene systems have now been identified in many other pathosystems, and the specific adaptation of pathogens to host taxa, such as those described as *formae speciales*, is generally accepted as “the outcome of coevolution” (25).

These relationships can be conceived of as arms races in which increased disease resistance develops in a host in response to increased virulence in a pathogen (10,74). The flux of resistant, rare host genotypes and susceptible, common genotypes has been studied most closely for obligate pathogens that have specific host ranges and possess the complementary gene-for-gene relationships described first by Flor (46), but it also occurs in nonobligate situations (25).

Coevolutionary interactions are spatially and temporally complex and thus can be difficult to study and document (10,16, 146). And there are reasons why coevolution might not develop between co-occurring hosts and pathogens, even when these are obligate relationships (122). For example, insufficient genetic variation may exist in the host or pathogen for coevolution to occur, or the pathogen may

not speciate at the same time as the host (122). Nonetheless, coevolution appears to be an important factor in the development of many pathosystems (17). Several criteria can be used to identify possible coevolved pathosystems (10,16,19,25,46, 53,57,62,129,136,146). These include:

- a limited, often specific host range for the pathogen;
- an original geographic distribution of the pathogen that overlaps with that of the host;
- the occurrence of significant disease resistance in the host’s primary center of origin;
- regional overlap of resistance and pathogenicity factors and phenotypes in the respective host and pathogen populations (i.e., geographic evidence for reciprocal selection);
- gene-for-gene relationships; and
- tandem speciation (aka parallel cladogenesis).

Most examples of supposed coevolved pathosystems possess some, but not all, of these attributes (25,40,92,112), and there are relatively few examples of unequivocal host–pathogen coevolution where unambiguous molecular data underpin the relationship (62,129). However, the numbers of unequivocal coevolved pathosystems will surely increase as greater sophistication is used in the identification of these relationships and the coevolution process is better understood. In the meantime, coevolution will remain a useful concept for the study of host–pathogen interactions.

Centers of origin, the enemy release hypothesis, and new-encounter diseases. The great plant explorer Vavilov (155) recognized different geographic regions in which important sets of crops plants were domesticated and utilized by primitive societies, and where, subsequently, ancient civilizations began. The concept of agricultural centers of origin has been criticized, refined, and more fully developed in recent years (33,56).

Although some of the centers that Vavilov (155) recognized might be questionable, centers of origin for domesticated crops are usually clear (76,128,135). Genetic diversity is often greatest in the primary centers (where the crop first evolved), but can also be considerable in secondary centers. In extreme cases, distinct types of host plants may be found in secondary centers: for example, the East African Highland cooking bananas, highly diversified in upland East Africa but not found or unrecognized in the primary Southeast Asian home of banana (71,134).

Given the heterogeneous nature of tropical environments, one might assume that tropical crops perform best where they evolved, i.e., under conditions to which they had adapted over time. In fact, significant production for many tropical crops occurs outside the native ranges (Table 3). Why is this so? Although several factors

have been proposed, the absence of coevolved plant pathogens often plays a significant role. When species display enhanced fitness in new habitats, they have often been “released” from important coevolved enemies (54,96).

The so-called “Enemy Release Hypothesis” has been used by ecologists to explain the development of weed species in new habitats. In an investigation of the hypothesis, Mitchell and Power (97) found 24% fewer viruses and 84% fewer rust, smut, and powdery mildew fungi on 473 nonendemic plant species in the United States than in their native habitats in Europe. Invasive weed species (those that were most fit) were more completely released from the pathogens (had fewer) than their nonweedy counterparts.

There are many examples of tropical crops that are most productive in non-native habitats (114,135). For some of these crops, the absence of a single or a few key pathogens is a pivotal reason for this productivity. The continued production of such crops in the new areas depends upon the continued exclusion of the pivotal (most dangerous) pathogens, and failure to do so can be costly. For example, the coevolved Sigatoka leafspot pathogens, *Mycosphaerella musicola* and *M. fijiensis*, dramatically affected banana (*Musa* spp.) production whenever they were reunited with their host in new production areas.

Other tropical perennial crops that have been released from destructive, coevolved pathogens in new production areas include:

- banana, major production of which occurs outside Southeast Asia where tropical race 4 of *F. oxysporum* f. sp. *cubense* does not occur (109);
- Para rubber, production of which predominates in Southeast Asia in the absence of South American leaf blight (40);
- pineapple, *Ananas comosus*, major production of which occurs where the coevolved fusariosis pathotype of *Fusarium guttiforme* is not found (117);
- coffee, *Coffea arabica* and *C. robusta*, most of which is produced outside Africa where coffee wilt disease (aka tracheomyces), caused by *Gibberella xylarioides* (anamorph: *Fusarium xylarioides*) is found (123) (dissemination of another coevolved disease, yellow rust, has had a major impact on *C. arabica* production worldwide) (92) (Fig. 1);
- cacao, *Theobroma cacao*, 85% of which is produced where the coevolved witches’-broom pathogen, *Moniliophthora* (syn. *Crinipellis*) *perniciosa*, does not occur (110) (Fig. 2); and
- oil palm, *Elaeis guineensis*, more than 90% of which is produced outside West Africa (42). Until recently, Fusarium wilt, caused by *F. oxysporum* f.

sp. *elaedis*, was found only in West Africa, where it coevolved with its host (45). Fusarium wilt has a major influence on oil palm production in Africa, and would undoubtedly impact the primary Southeast Asian production centers if it was moved there.

As mentioned above, resistant parents for coevolved hosts are often found in the respective centers of origin (81,136). Prospecting in these areas for resistant

parents is a common strategy used by breeding programs. Unfortunately, habitat destruction, deforestation, and mismanagement cause losses of these genetic resources (21,30,40). The extinction of these valuable sources of disease and pest resistance, productivity, and environmental adaptability is a serious problem.

Although resistant parents are usually available for the coevolved diseases, they may not be available for new-encounter diseases. Thus, new-encounter diseases

can be just as devastating as coevolved diseases, but may be more difficult to control. Serious new-encounter examples for which little conventional resistance is known include Phytophthora root rot of avocado, caused by *P. cinnamomi* (166), and citrus greening, caused by three different 'Candidatus Liberobacter' spp. (S. Halbert, *personal communication*).

New-encounter diseases develop when a plant is confronted with a pathogen with which it has not had an evolutionary

Table 3. Selected coevolved and new encounter pathogens of tropical perennial crops

Crop	Relative production ^x	Pathogen (disease) ^w		References
		Coevolved	New encounter	
Avocado	Moderate	* <i>Sphaceloma perseae</i> (scab), <i>Mycosphaerella perseae</i> (silver spot)	* <i>Phytophthora cinnamomi</i> (Phytophthora root rot)	39, 95, 166
Banana	Major	* <i>Fusarium oxysporum</i> f. sp. <i>cubense</i> (Panama disease), * <i>Mycosphaerella fijiensis</i> and <i>M. musicola</i> (Sigatoka leafspots), <i>Uredo musae</i> (rust)	* <i>Ralstonia solanacearum</i> phylotype II (Moko disease), * <i>Xanthomonas campestris</i> pv. <i>musaeorum</i> (xanthomonas bacterial wilt)	13, 43, 112, 140, 141, 145, 149, 151, 164 ^y
Cacao	Major	* <i>Moniliophthora perniciosa</i> (witches'-broom)	* <i>Moniliophthora rorei</i> (frosty pod), * <i>Cacao swollen shoot virus</i> (swollen shoot), * <i>Oncobasidium theobromae</i> (vascular streak dieback), * <i>Phytophthora megakarya</i> (black pod), * <i>Ceratocystis cacaofunesta</i> (vascular wilt)	8, 19, 37, 40, 41, 52
Cinchona	Major	<i>Phytophthora quininea</i>	<i>Phytophthora cinnamomi</i> , <i>Phytophthora nicotianae</i>	39, 161
Citrus	Major		*'Candidatus Liberobacter africanus', 'Candidatus Liberobacter asiaticus' and 'Candidatus Liberobacter americanus' (huanglongbing [greening]) ^z , <i>Xylella fastidiosa</i> (variegated chlorosis), phytoplasma (witches'-broom of lime)	115, 150
Coconut	Moderate		*Phytoplasmas (lethal yellowing, Awka wilt, coconut lethal disease, etc.), <i>Bursaphelenchus cocophilus</i> (red ring), <i>Phytophthora katsurae</i> (bud rot), <i>Phytomonas</i> (hart rot)	58
Coffee, <i>Coffea arabica</i>	Major	* <i>Gibberella (Fusarium) xyloarioides</i> (tracheomyces), <i>Hemileia coffeicola</i> (grey rust), * <i>Hemileia vastatrix</i> (yellow leaf rust)	* <i>Mycena citricolor</i> (ojo de gallo), <i>Xylella fastidiosa</i> (variegated chlorosis)	92, 115, 118, 123, 133, 152
Eucalyptus	Major		<i>Puccinia psidii</i> (rust)	24
Guava, <i>Psidium guajava</i>	Moderate	<i>Puccinia psidii</i> (rust)	<i>Penicillium vermoesini</i> ? (guava wilt)	24, 83
Mango	Moderate	* <i>Fusarium mangiferae</i> (malformation)	* <i>Fusarium sterilihyposum</i> and * <i>Fusarium</i> sp. (malformation); * <i>Ceratocystis fimbriata</i> (seca, sudden wilt)	3, 89, 106, and footnote y
Oil palm	Major	* <i>Fusarium oxysporum</i> f. sp. <i>elaedis</i> (Fusarium wilt)	* <i>Thielaviopsis paradoxa</i> ? (pudricion cogilla [bud rot]), <i>Phytomonas</i> (marchitez sopresiva), * <i>Ganoderma boninense</i> (ganoderma butt rot), *Phytoplasma? (marchitez letal [lethal wilt])	12, 31, 36, 45, 104
Papaya	Major		* <i>Papaya ringspot virus</i> (papaya ringspot), * <i>Phytophthora palmivora</i> (fruit, root, and stem rot), *'Candidatus Phytoplasma australasia' (papaya dieback, yellow crinkle and mosaic)	9, 103
Pineapple	Major	* <i>Fusarium guttiforme</i> (fusariosis)		117
Rubber	Major	* <i>Microcyclus ulei</i> (South American leaf blight)		40

^w Coevolved and new encounter pathogens are defined using criteria listed in the text. Those marked with an asterisk are major problems.

^x Relative production: Major = more than 70% of all production for crop occurs outside endemic range(s); moderate = 30 to 69%; minor = 5 to 29%; negligible = less than 5%.

^y C. S. Lima, L. H. Pfenning, S. S. Costa, M. A. Campos, and J. F. Leslie, *unpublished*.

^z The *Candidatus* species that are associated with citrus greening (huanglongbing) appear to be new encounters in Africa (*Liberobacter africanus*), Asia (originally India?) (*Liberobacter asiaticus*), and Brazil (*Liberobacter americanus*) (S. Halbert, *personal communication*).

history (102). Two types of new encounters have been described (17).

The first, apparently uncommon (or at least not commonly documented), results from an evolutionary host jump. Genetic changes in the pathogen (somatic hybridization, chromosome loss, and recombination are among the mechanisms) result in its adaptation to a co-occurring, previously nonsusceptible host (9,122,138).

The second kind of host jump results from dissemination of either the host or pathogen to effect a new interaction (14,57). Often, the original host of the new-encounter pathogen is not known; examples include:

- Ceratocystis wilt of cacao, caused by *Ceratocystis cacaofunesta* in tropical America (8,37);
- seca or sudden decline of mango caused in Brazil and Oman by *Ceratocystis fimbriata* (3,106) (Fig. 3);
- wilt of guava, *Psidium guajava*, caused in Malaysia, South Africa, and Taiwan by a fungus with unclear taxonomic affiliations (83);
- witches'-broom of lime, *Citrus aurantifolia*, caused in the Middle East by a phytoplasma (150) (Fig. 4);
- mango malformation, caused in Brazil (and possibly elsewhere in the Americas) by *Fusarium sterilihyphosum*, an unnamed mating population of the *Gibberella fujikuroi* species complex, and possibly other taxa (119; C. S. Lima, L. H. Pfenning, S. S. Costa, M. A. Campos, and J. F. Leslie, unpublished) (Fig. 5);
- vascular streak dieback of cacao, caused in Asia by *Oncobasidium theobromae* (52); and
- xanthomonas wilt of banana, caused in Africa by *Xanthomonas campestris* pv. *musaeorum* (it was reported initially on a banana relative, *Ensete ventricosum*, but it is not clear whether this first host was coevolved or new encounter [149,151,164]) (Fig. 6).

When the original hosts of new-encounter diseases are known, they are usually closely related to the newly encountered host. For example:

- *Colletotrichum kahawae*, cause of coffee berry disease, originated on *Coffea eugenioides*, a close relative (precursor?) of *C. arabica* (152) (Fig. 7);
- *Moniliophthora rorei*, cause of frosty pod of cacao, probably originated on *Theobroma gileri* (40) (Fig. 8);
- *Ralstonia solanacearum* phylotype II, cause of Moko disease of banana, evolved on banana relatives in the Americas, *Heliconia* spp. (13,43) (Fig. 6);
- *Ganoderma boninense*, the basal stem rot pathogen of African oil palm,

originated on coconut palm, *Cocos nucifera*, in Asia (36,104); and

- *Puccinia psidii*, cause of rust of eucalyptus, *Eucalyptus* spp., originated on other genera and species in the Myrtaceae in the Americas (24).

Although new encounters usually occur over great distances, this is not always the case, and there are instances when new-encounter pathogens evolved in close proximity to the new-encounter host. For example, *M. rorei* probably originated on

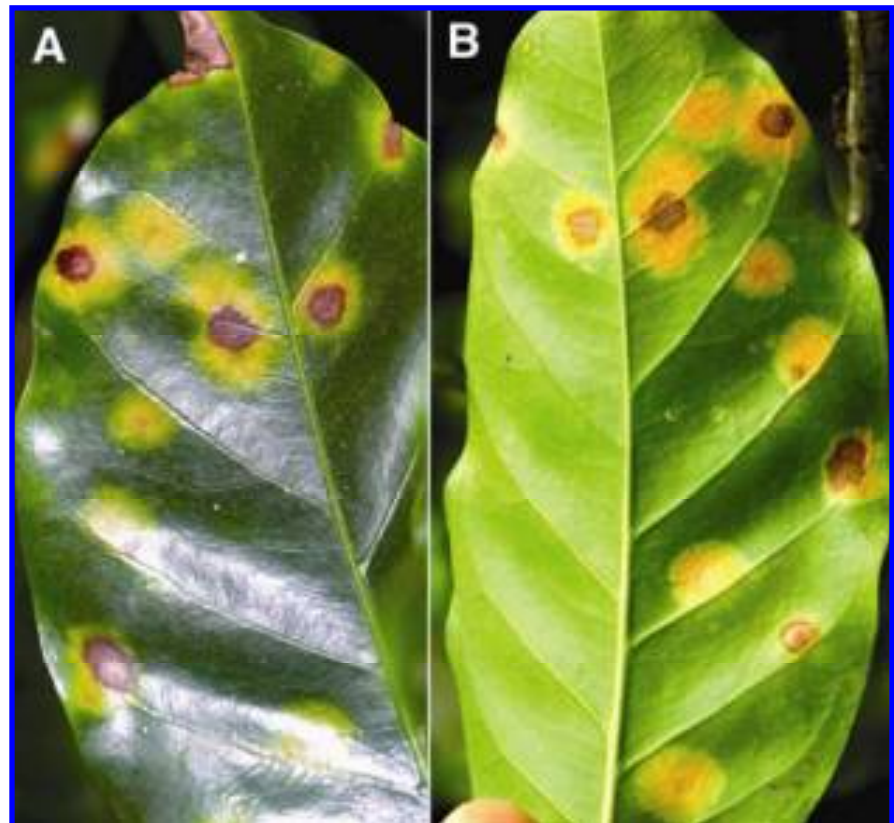


Fig. 1. A, Adaxial and B, abaxial surface of a leaf of coffee, *Coffea arabica*, affected by yellow rust, caused by *Hemileia vastatrix*. Rust caused little damage in natural, heterogeneous stands of coffee in Ethiopia, and in the arid Arabian Peninsula where the crop was first produced outside Africa. However, beginning in the late 1800s in humid Sri Lanka and India, the disease started to spread and cause serious damage in monoculture production.



Fig. 2. Witches'-broom, caused by the hemibiotroph *Moniliophthora perniciosa*, is the most serious coevolved disease of cacao. A, Hypertrophied brooms are induced during the pathogen's biotrophic phase. B, Brooms die as the disease transitions from the biotrophic to the necrotic phase. C, Basidiomes of the pathogen form later on necrotic tissues, such as this pod.

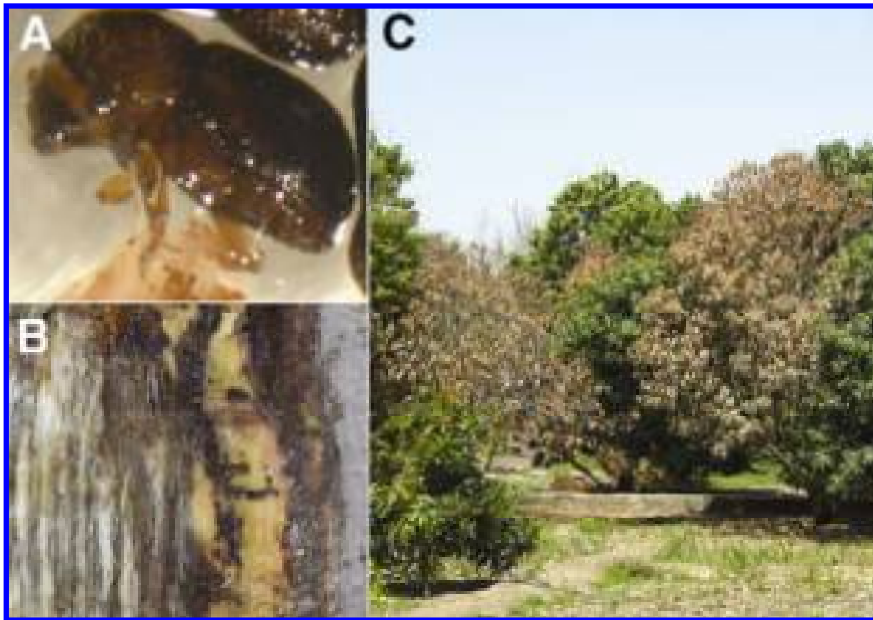


Fig. 3. The new-encounter disease known as *seca* and Recife sickness in Brazil and sudden wilt in Oman is caused by *Ceratocystis fimbriata* and vectored by A, the scolytid beetle, *Hypocryphalus mangiferae*. B, Internal symptoms caused by the disease and galleries of *H. mangiferae*. C, Unilateral death of portions of affected trees in Oman; ultimately trees are killed. This disease is an example of failed quarantine measures, in that it was restricted to Brazil until it was recently introduced into Pakistan and Oman; it poses a grave threat to a primary center of mango germplasm in India.

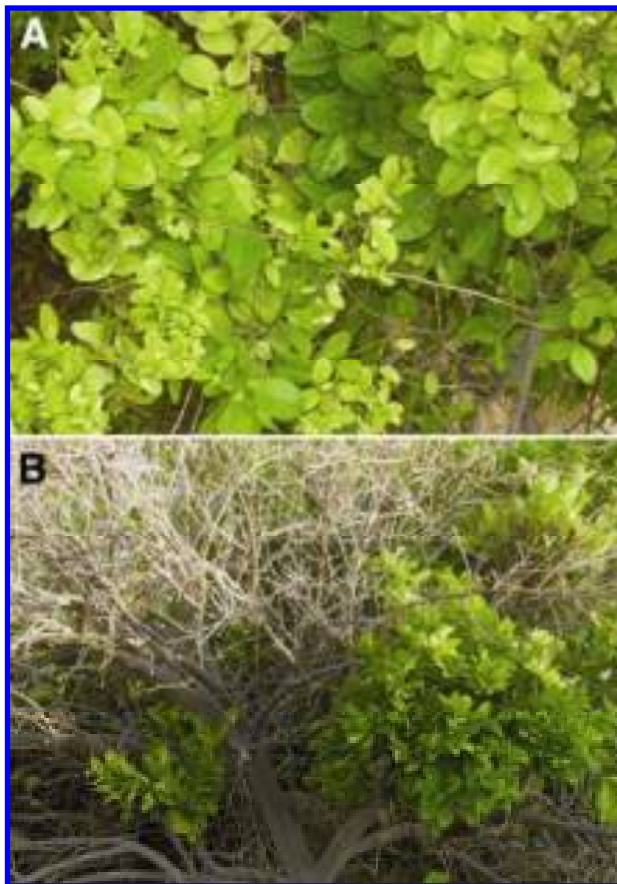


Fig. 4. Lime witches'-broom is one of several serious new-encounter diseases of citrus (here on *Citrus aurantifolia*). Found in the Middle East and caused by a phytoplasma, it initially, A, dwarfs and malforms terminal portions of the canopy and, B, later kills large portions of the tree.

the western flank of the Andes, a short distance from the cacao center on the range's eastern flank (40).

Disease Management in Tropical Perennial Crops

To devise effective management strategies, it is usually necessary to understand the disease's etiology and epidemiology. When causal agents are not known, or when they cannot be cultured and used to artificially induce disease, it is usually not possible to test treatment efficacy in a controlled manner. Two debilitating citrus diseases provide examples: blight, which has an unknown etiology, and greening, which has at least three unculturable, putative agents (150). And even when causal agents are known, unclear epidemiologies or an inability to reproduce symptoms artificially with a given agent are significant handicaps. Both of these factors contribute to management problems with basal stem rot of oil palm, a disease that kills as many as 70% of the palms in plantations in Indonesia and Malaysia (36,104).

In general, effective disease management relies on a delay in the onset or reduction in the initial levels of disease (x_0), or a reduction in the rate at which disease develops over time (r) (154,165). Below, I briefly relate these epidemiological principles to the following tactics: avoidance, exclusion, and eradication of causal agents; protection of, or development of resistance in, the host plant; and treatment of affected plants.

Avoidance. Planting site selection is an important first step in establishing a production area, and can be an important tactic for disease avoidance (101,165). In general, the conditions under which disease development is favored or hosts are predisposed to disease development should be considered. For example, swamp spot of banana, caused by *Deightonella torulosa*, is exacerbated in low-lying and poorly drained situations, as are numerous root rots that are caused by stramenopiles (39,107,141,153) (Fig. 9). By avoiding chronically wet sites, it is possible to reduce x_0 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 (131). 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 (101). For example, Phytophthora root rot of avocado is most severe between 15 and 27°C, temperatures that are also optimum for the host (166). 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, caused by *Xanthomonas* sp. pv. *mangifer*

aeindicae, or biotic, as for the enhanced development of citrus canker in leaves damaged by the citrus leafminer (48,150). Managing the predisposing factors is always helpful.

The importance of using disease-free planting materials cannot be overstated, and any measure or legislation that would produce disease/pathogen free materials and disseminate them to growers would be useful (66). For example, clean nursery stock and budwood schemes are hallmarks of successful citrus programs (113).

Vegetative propagules can harbor bacteria, fungi, nematodes, viruses, and viroids, and it is with them that many economically important pathogens are moved and established (65). True seed are less apt to carry pathogens, but they can also pose significant risks. The key with both vegetative materials and true seed is to know what diseases can be moved in these ways on a given crop.

Tissue-culture plantlets should be used whenever possible, since they are free of fungal, bacterial, and nematode pathogens ($x_0 = 0$) (66). 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 ref. 84).

Many diseases of perennial crops originate in propagation nurseries, and soil-borne diseases whose symptoms are not readily apparent can be most problematic. *Phytophthora* root rot of avocado is a good example. *P. cinnamomi* originated in New Guinea, but has been disseminated worldwide in contaminated planting stock (166). Its establishment in new avocado orchards usually results from planting trees that were infected in the nursery (95).

Exclusion. Diverse tactics exist for the exclusion of plant pathogens (66,101). Although the idea that “there is no disease without the pathogen” is a simple one, excluding pathogens from production areas ($x_0 = 0$) can be difficult. When it is possible, exclusion is a most cost-effective disease management strategy.

The early detection and accurate identification of pathogens are often important first steps in exclusion, and the certification of pathogen-free status and safe movement of germplasm rely on their success (66,101,113). All too frequently, pathogens move via human intervention. 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 (66,88,113,143). Unfortunately, these rules are not always enforced sufficiently to ensure border safety, and there are numerous examples of destructive agents moving despite quarantines. The recent accidental introduction of *Xanthomonas axonopodis* pv. *citri* into citrus-

growing areas in Florida and Queensland, Australia, and the purposeful movement of *Moniliophthora perniciosa* into cacao plantations in Bahia, Brazil, are good examples of the anthropogenic dissemination of harmful plant pathogens (51,65,72,73). The removal of trade barriers may also be problematic; the concerns that nonendemic pathotypes of *Guignardia musae* and *Ralstonia solanacearum* might be introduced into Australia if Philippine bananas are shipped to this country are examples (70,113).

Pathogens that are moved in debris and on machinery, tools, and other implements can be excluded by surface disinfection with chemical and physical measures (Fig. 10). Likewise, seed and planting material can be treated to kill pathogens. Heat treatment (thermotherapy) of vegetative propagation materials is useful against bacteria, fungi, nematode, and virus pathogens. However, there must be a significant difference between the temperatures at which a pathogen dies and the host is adversely affected. This can be a fine line, and heat-

sensitive plants can be damaged if exacting temperature controls are not available. Only some pathogens lend themselves to this approach, and most of the successful examples that are available are for annual and/or temperate crops (101). However, heat treatment is effective for some tropical perennials. For example, heat treatment eliminates the ratoon stunt pathogen, *Clavibacter xyli* subsp. *xyli*, from sugarcane cuttings (50), and the burrowing nematode, *Radopholus similis*, from banana suckers (126).

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 (77), surface disinfection with chlorine or fungicides is most frequent. For seedborne pathogens of quarantine concern, such as *Fusarium oxysporum* f. sp. *elaedis* (*Fusarium* wilt of oil palm), extra precautions are needed to ensure that all seedborne inoculum is killed or intercepted (45). This has been of vital concern when oil palm seed from Africa has been disseminated. In

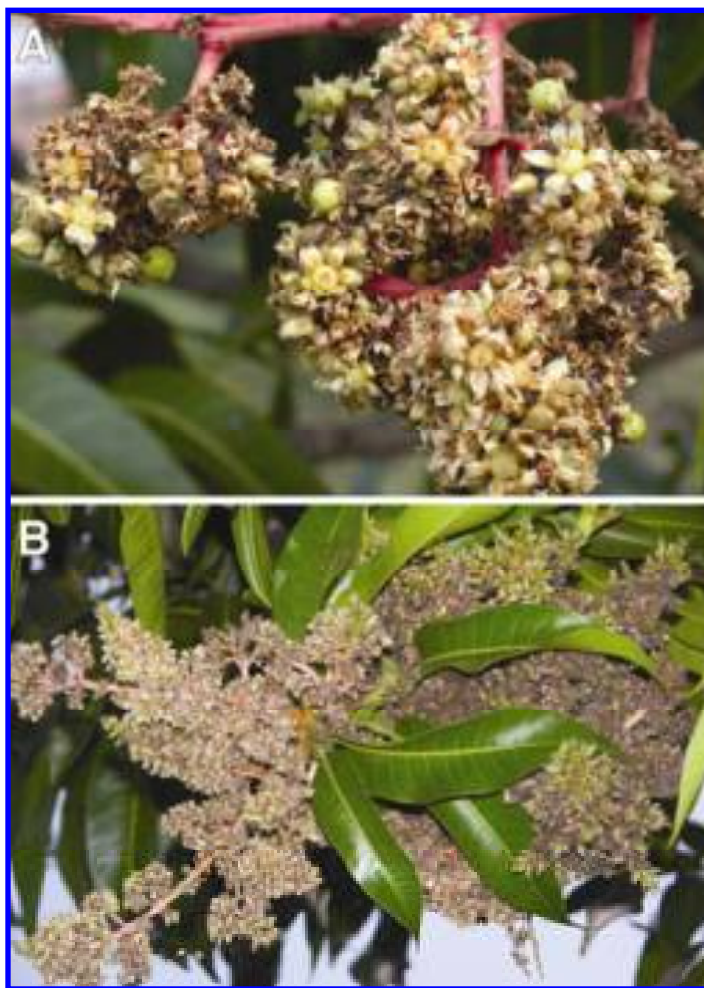


Fig. 5. Mango malformation is caused by several different fungi. In most of the world, including a presumed coevolved center in India, *Fusarium mangiferae* is responsible for the disease. However, in tropical America, *F. sterilhyphosum*, an unnamed mating population of the *Gibberella fujikuroi* species complex, and possibly other taxa cause and/or are associated with malformation. Note the similar panicle symptoms induced by A, *F. mangiferae* in Florida and B, *Fusarium* sp. in Mexico.

these cases, seed have been vacuum infiltrated with fungicides and the resultant seedlings placed in intermediate (UK) and postentry (Malaysia) quarantine before release to breeding programs.

Pathogen vectors can also be eliminated to exclude pathogens of concern, but there are obvious requirements, including knowledge of which vectors are problematic, where they reside, and how and whether they can be managed effectively. As for the causal agents, complete elimination of vectors is often difficult.

Eradication. If pathogen exclusion has failed or is not possible, a different set of strategies is needed. These measures are diverse, always more expensive than pathogen exclusion, and seldom entirely effective. The recent investment of ca. \$1 billion to eradicate citrus canker in Florida is an extreme example of the expense of an unsuccessful effort to eliminate a pathogen (51; T. Gottwald, *personal communication*). Among these options, pathogen

eradication is often considered first. Although the goal of eradication is to reduce x_0 to 0, in practice these measures are most often rate limiting.

When they are significant reservoirs of inoculum, alternate (i.e., hosts of heteroecious rusts) and alternative hosts are removed from plantations and destroyed. Disease pressure is usually reduced in such cases and, when alternative host species are involved, is most effective when their host ranges are limited. However, pathogens with wide host ranges can also be managed in this manner: for example, weed hosts of *Cucumber mosaic virus* in banana plantations (85). The effectiveness of removing alternate and 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 regional barberry eradication programs that were instituted to manage wheat stem rust is a prominent, albeit annual and nontropical, example of

extreme measures that were used for a highly mobile pathogen on a widely dispersed alternate host [18]).

Sanitation, 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 (Fig. 11A), removed from plantations, and destroyed (Fig. 11B) (145). Successful control can also result

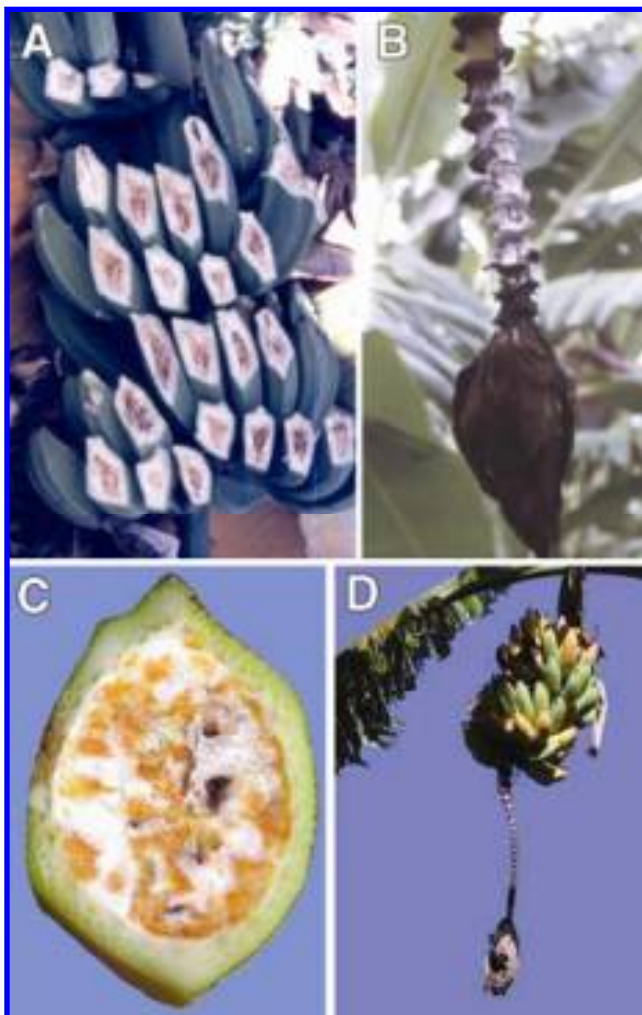


Fig. 6. Two new-encounter diseases of banana, A and B, Moko disease, caused by phylotype II of *Ralstonia solanacearum*, and C and D, xanthomonas bacterial wilt, caused by *Xanthomonas campestris* pv. *musaeorum*, cause similar symptoms and have similar epidemiologies, despite their different geographic origins (respectively, tropical America and Ethiopia) and etiologies. Photos A and B courtesy of I. W. Buddenhagen, and C and D courtesy of Eric Boa.



Fig. 7. *Colletotrichum kahawae*, cause of coffee berry disease, probably coevolved with a close relative of *Coffea arabica*, *C. eugenioides*.



Fig. 8. The new-encounter disease frosty pod, caused by *Moniliophthora rorei*, is the most destructive disease of cacao, due in large part to the billions of thick-walled, long-lived infective spores that are produced on affected pods. Dissemination of frosty pod and witches'-broom (Fig. 2) to the important West African production areas would be disastrous for the world's chocolate trades.

when specific organs of the host are removed. For example, the black pod and frosty pod diseases of cacao can be effectively and economically managed via the removal of affected pods (137). 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* spp., *Ganoderma* spp., *Phellinus noxious*, and *Rigidoporus lignosus* are among the most notorious examples of these pathogens because they are good saprophytes and colonize dead roots and stumps in disturbed sites (99,107). Once affected materials are removed from plantations, it is important that they be destroyed (Fig. 11B). "Cull piles" are significant sources of inoculum for many diseases.

Different biocidal measures can be used to eliminate pathogens from soil. Their impacts range from nonspecific to somewhat specific, and due to their expense, they are used only for high-value crops. Flooding and broad-spectrum fumigants, such as methyl bromide + chloropicrin, eliminate large portions of the soil biota, resulting in what is essentially a biological vacuum. 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 (59,90,140). 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) (75,101). Most of these treatments, including 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.

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 (102). Those that are highly susceptible to damaging diseases are among the most prominent examples; they include: banana (primarily Sigatoka leafspots), citrus (several fruit and foliar diseases), coffee (rust), and mango (primarily anthracnose) (5,7,105,107,133).

Vector control can be used to indirectly protect the host from the pathogen, but there are several caveats. Pesticide applica-

tions that are needed to effect disease control may not be cost effective unless the crop is valuable, the treatments are highly effective, and region-wide programs are utilized. The successful management of citrus greening in South Africa is a relevant example, in that large areas are treated for the psyllid vector (82). And even 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 that do not establish on papaya (it is not a preferred host), is one such disease (103). Some vectors reside in protected locations that are relatively inaccessible to pesticides and thus are 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 (107). Finally, efficacious measures for controlling vectors may not



Fig. 9. 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*.



Fig. 10. Precautions against the movement of subtropical race 4 of *Fusarium oxysporum* f. sp. *ubense* in South Africa: A, Altus Viljoen disinfects the soles of Mike Rutherford's shoes before he moves from an infested area, and B, the pathogen is isolated in a former production area by a fence; note the fine-mesh barbed wire at the fence's base for small animals.

be available. For example, papaya bunchy top was effectively managed with DDT, since it controlled the leafhopper vectors, *Empoasca papayae* and *E. stevensi*; however, an effective replacement for this insecticide has not been identified (28).

Other issues that surround pesticide usage will not be covered here for lack of space, including: different chemistries that are available and their spectrums of activity; the development and use of disease forecasting models; application formulations, equipment, and methods; the use of spray oils, spreader stickers, and other amendments; applicator safety; and environmental concerns that are associated with pesticide usage (113).

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 (101). Shade reduces the severity of black Sigatoka of banana, but it promotes the development of diseases that require high humidity or free moisture, such as black pod of cacao and coffee berry disease (107,141,152). In the later cases, orienting rows such that prevailing winds and the morning sun have the greatest opportunity to dry the canopy can be helpful (111).

Diverse edaphic modifications are used. Improved drainage and the use of mounds or beds can significantly reduce stramenopile-induced root diseases (22,39,95,147). 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* (101). 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 (14). Although it may be possible to change a soil's pH with amendments (e.g., lime to raise the pH of acidic soils or

sulfur to acidify those that are basic), it is not possible to do so with all soils. For example, it is virtually impossible to lower the pH of calcareous soils due to their buffering capacity.

Host nutrition and fertilization practices can have a large impact on disease development (27,101). Although most examples are for annual or short-season crops, some perennials that are grown in the tropics have been studied. The amounts of certain elements can be important; for example, applications of silicon-based amendments decreased the severity of ring spot of sugarcane (27). And the forms of nutrients can be important. For example, ammoniacal nitrogen increased the severity of Phytophthora root rot of citrus, whereas nitrate nitrogen decreased its severity (94).

Physical exclusion is useful in some situations. Greenhouse production of banana in Morocco creates a requisite warm environment, but also 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, but also assist postharvest 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 (Fig. 10B). 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 (149).

Biological disease control measures are receiving increased attention in tropical perennial crops due to declines in the numbers of pesticides that are available, decreased efficacy of some pesticides due to resistance, and concerns about human and environmental safety that are associated with pesticide use (69,108,124,125). Biocontrol of postharvest diseases of tropical fruits, caused mainly by fungi, has been

studied extensively (69). The unique niches that are protected and the postharvest 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 (69,78,79). 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 (163) in much the same way that mild strains of *Citrus tristeza virus* have been used to protect citrus (150).

Biological control of plant disease is never easy, and can be especially difficult for systemic diseases that increase in severity over the lifespan of a given planting. Research on the biological control of Panama disease illustrates the point with a crop that is typically grown for several years (108). Although numerous researchers have investigated the biological control of this disease, to date an 18% annual loss has been the best result achieved that has been reported in a refereed journal (127). This loss rate might be acceptable in a short-season crop, but would be disastrous in a perennial crop like banana (for example, a compounded loss of 63% would result after 5 years of ratoon production).

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 (136). For an interesting synopsis on disease resistance and breeding in tropical crops, see Buddenhagen (14).

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 (81,136). Many breeding success stories result from the use of such resistance.

Useful resistance may be available to some new-encounter diseases. For example, cacao parents that resist swollen shoot and vascular streak dieback are important in breeding programs in, respectively, Ghana and Papua New Guinea (R. J. Schnell, *personal communication*). However, useful genes may be infrequent in the new-encounter host crop. The poor resistance that exists in new-encounter situations can be circumvented if the original host of the new-encounter disease is sexually compatible with the new-encounter host. Intertaxon hybrids may be immediately useful. For example, interspecific hybrids between African oil palm, *E.*



Fig. 11. The management of banana bunchy top, caused by *Banana bunchy top virus*, in Egypt and elsewhere relies on: **A**, frequently identifying symptomatic plants, and **B**, removing and destroying such plants. Banana cannot be grown successfully wherever this disease is found and these practices are not followed.

guineensis, and American oil palm, *E. oleifera*, resist two new-encounter diseases in the Western Hemisphere, bud rot and lethal wilt (12,31) (Fig. 12). Or resistance genes can be introgressed into the host crop. 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 (121).

The need for and usefulness of resistant perennial crops in the tropics should consider the type of disease that is addressed.

Although they may be critical for foliar diseases that progress rapidly (high *r*), susceptible genotypes may be used for years before they need to be replaced if a slow-developing soilborne disease is involved. McDonald and Linde (93) classified the durability of host resistance based on the life strategies and niches of the causal agents.

Genetic resistance obtained via conventional breeding is often classified as vertical (usually controlled by one or a few major genes) or horizontal (several genes) (93,154). Much has been written about the

dangers of vertical resistance. Although high levels of resistance can be achieved with it, it is almost always pathotype specific. Its use in perennial crops is dangerous since it can be easily overcome by the evolution or selection of virulent pathotypes. Coffee/*Hemileia vastatrix* and rubber/*Microcyclus ulei* are two tropical perennial pathosystems for which vertical resistance has not been durable (80,118, 133,136).

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 genetically variable pathogens with both sexual and asexual life cycles, i.e., those classified by McDonald and Linde (93) as having "a high evolutionary potential." 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 (93,136).

When considering horizontal resistance, disease impact must be taken into account. Horizontal resistance in perennial crops might be valuable against nonlethal diseases but less so against those that kill plants. Coffee improvement schemes have developed both vertical resistance to rust in *C. arabica* selections and hybrids as well as horizontal resistance in intra- and interspecific hybrids (the other parental species, *C. canephora*, is highly tolerant) (118,133).

Genetic transformation for disease resistance (the creation of Genetically Modified Organisms, GMOs) can be quite effective (93,143). 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* (44). 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.

Treatment of diseased plants. Diseased plants can be treated effectively with various curative (systemic) chemicals, and by the removal of affected portions of the host (i.e., surgery) to reduce inoculum levels. These are rate-limiting measures.

Since the development of the first systemic fungicides, an increasing number of these compounds have been developed for

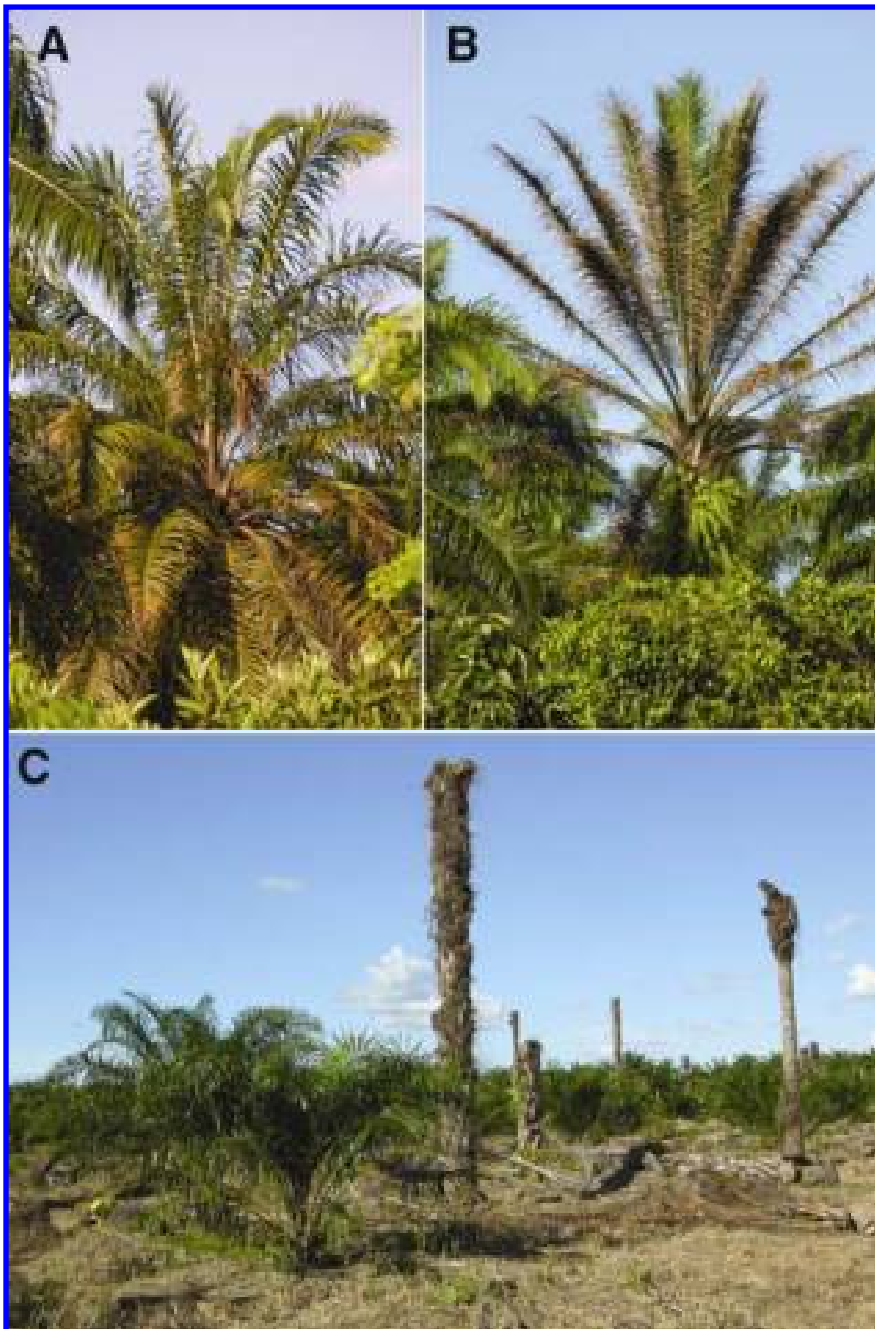


Fig. 12. The new-encounter disease lethal wilt (marchitez letal) rapidly kills oil palm in the Llanos region of Colombia. A and B, From the first stages of the disease until C, death, usually takes less than 6 months. Although its cause is not known, useful resistance is found in the American oil palm, *Elaeis oleifera*, which has been utilized in interspecific hybrids with *E. guineensis* (note that hybrids have been planted in the disease focus in C).

agricultural use. Benzimidazoles (1973), triazoles (1984), and strobilurins (1997) are among the most common systemic fungicides. Their primary activity is as protectants, but a portion of the applied compound is absorbed into treated organs. The curative, “kick-back” impact of these compounds revolutionized the management of many diseases (142).

An unfortunate attribute of some of the most effective systemic fungicides is the ease with which their efficacy is lost; their specific modes of action often make them vulnerable to the development of resistance. Black Sigatoka management in the Americas provides examples (105). Within 2 to 3 years of the introduction of benomyl for the control of black Sigatoka, resistance in *M. fijiensis* began to be observed

in Central America, and by the late 1970s the chemical could no longer be used effectively in many areas (142). More recently, strobilurins have become increasingly ineffective in tropical America against this disease (68,105).

Brent and Hollomon (11) discussed the propensity of different classes of fungicides to lose effectiveness over time. They noted a wide range in the inherent risk of resistance to develop in different classes. Among the systemics that have been used against black Sigatoka, the benzimidazoles were ranked as high risk and the strobilurins as moderate. They also classified the risk of resistance developing in various pathosystems. The banana/*M. fijiensis* system was classified as high risk since the pathogen had a short generation time, sporulated abundantly, and had a sexual cycle that facilitated the development of resistance. Working groups of the Fungicide Resistance Action Committee (FRAC) of the Global Crop Protection Federation (an international consortium of agrochemical producers) have created use guidelines to prolong the effective life of vulnerable fungicides (11).

Two systemic pesticides, metalaxyl and fosetyl-Al (and its phosphonate derivatives), are effective against stramenopiles (23). 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 (95,107). 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 trunk injected. Phytophthora root rot of avocado and *P. palmivora*-induced diseases of other tropical perennials are among the diseases that are managed effectively via trunk injection (35).

Conclusions

Ideally, crop production entails a holistic view of the health and productivity of a given crop. Disease management should be considered as part of an integrated approach to crop production that also includes the nutrition, water, and environmental needs of the crop, and its economic constraints.

Just as diverse facets of plant health should be considered during production, disease management should also embrace a holistic view. Diseases of tropical perennials that can be managed effectively with a single tool are rare, and in most cases an integrated approach should be considered that utilizes several different approaches. The integrated management of Phytophthora root rot of avocado is an excellent example of how the concerted use of hygiene and sanitation, cultural and biologi-

cal controls, resistance, and pesticides could be used to manage a most difficult disease of a tropical perennial crop (22).

The management of diseases of tropical perennials is one of the greatest challenges in production agriculture. Long-term criteria must be used to judge the efficacy of the chosen strategies due in large part to the polycyclic nature of these diseases, the corresponding compound interest increase in disease that develops over time, and the disease-conducive environments that prevail in the tropics. Diverse factors that are mediated by time and money are far more critical for these problems than for those that face producers of other crops. Disease management strategies in tropical perennials must be effective and durable, yet responsive to changing environmental and market conditions. It is difficult to conceive of a more interesting and difficult set of problems in plant pathology.

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