Fungal and Oomycete Diseases of Tropical Tree Fruit Crops

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Abstract

The tropics produce a range of fruit from tree crops that cannot be grown in colder climates. Bananas, mangos, several nuts, spices, coffee, and cacao are widely traded and much sought after around the world. However, the sustainable production of these tropical tree fruit crops faces significant challenges. Among these, losses due to pests and diseases play a large part in reducing yields, quality, and profitability. Using bananas and cacao as key examples, we outline some of the reasons fungal and oomycete diseases cause such significant losses to tropical tree crops. Cultivation of monocultures derived from limited genetic diversity, environmental conditions conducive for disease development, high levels of disease incidence and severity, a lack of disease resistance in planting materials, shortages of labor, and inadequate infrastructure and investment pose significant challenges, especially for smallholder producers. The expansion of travel and trade has given rise to emerging infectious plant diseases that add further insecurity and pressure. We conclude that holistic actions are needed on multiple fronts to address the growing problem of disease in tropical fruit tree crops.

INTRODUCTION

Many of the fruits, nuts, spices, and edible oils consumed in the world are produced from tree crops grown in the tropics. Avocado, bananas, citrus, mangos, and durians are eaten fresh; nuts, such as cashews, the brazil nut, and macadamias, and spices, such as pepper and nutmeg, are dried; coffee and cocoa seeds are fermented, dried, and roasted; and oil palm fruit and coconuts are pressed to obtain the oil.

Most of these crops were domesticated in ancient times near their centers of origin (53), whereas a few, such as macadamia, have been domesticated only recently (51). The Western European conquest of the New World in the fifteenth century disseminated many tree crops across the tropics. This intercontinental exchange of plant and animal species popularly known as the Columbian Exchange (25) was supported by a systematic approach to economic botany, involving botanic gardens that played a pivotal role in acquiring, distributing, and commercializing many new crops (14). The Columbian Exchange has over the past four centuries given rise to major changes in people's diets around the world to such a degree that the vast majority of human dietary needs in most parts of the world are now met by introduced plant species (64).

One important reason for this dependence has been the high return on investment in the tropics that results from fertile virgin rainforest soils and favorable microclimates [together these are called the forest rent (110)] as well as relative freedom from coevolved pests and diseases when crops are grown outside their center of origin. However, these benefits fade with time, and pests and diseases increase in importance because of their natural dispersal abilities (15) and intercontinental movement as part of the Columbian Exchange. Improvements in transport infrastructure during the Industrial Revolution, including canals, steam ships, and railway networks, followed by the construction of a road infrastructure and, more recently, air travel, have ushered in an era of globalization (66). Significant increases in the frequency and volume of travel and trade have given rise to a dramatic increase in the global dissemination of pathogens (4, 13, 81).

Not only did coevolved pathogens follow their hosts to new environments, but introduced crops encountered new pathogens. This created a double threat of emerging infectious plant diseases that has heightened in the past few decades (38) and not only affects food crops but has also shown up in natural ecosystems, where loss of biodiversity has been caused by introduced diseases such as chestnut blight (3), sudden oak death (107), and Dutch elm disease in the United States (45), *Phytophthora* dieback in Australia (17, 138), and ash dieback in Europe (92).

PERENNIAL FRUIT CROPS IN THE TROPICS

Tropical habitats vary, often over short distances, from wet and humid tropical lowlands, savannahs, and deserts to alpine landscapes. Climatic conditions range from hot or mild humid weather all year round to seasonal wet and dry periods. Vavilov's pioneering work identifying centers of crop diversity and centers of domestication (134) showed that a large number of the plants we use in agriculture originated and were domesticated in mountainous areas in the tropics, where these ecoclines often overlap (52, 53). The wide range of microclimates, rainfalls, and temperatures found in the mountainous tropics promotes genetic diversification through mutation, selection, and adaptation (56, 141). Although many annual crops first domesticated there are now widely cultivated as summer crops in temperate zones, sensitivity to cold restricts the wider cultivation of tropical perennial crops.

The cultivation of perennial fruit crops in the tropics varies from semisubsistence smallholder foraging to large-scale industrial plantations. There are many reasons why the control of fungal and oomycete diseases in tropical perennial crops is a major challenge. Consistently warm temperatures, high rainfall, and high relative humidity with long periods of leaf wetness create an extended window for pathogens to germinate, infect, colonize, and sporulate on susceptible host plant tissues, which may be present all year round. Favorable environments and the evergreen nature of the canopy mean pathogen dormancy is not essential, creating an opportunity for the pathogen to remain active. The cultivation of perennial plants requires the grower to protect this year's fruit while at the same time keeping the tree healthy for many years to protect productive capacity without a break in the disease cycle.

Pathogens such as *Phytophthora palmivora* affect multiple plant parts, including roots, stems, branches, flowers, leaves, and fruit, of hosts like cacao and durian (33). Once established in a plantation, such pathogens are difficult to control, as primary inoculum is omnipresent and wet weather conditions trigger the rapid propagation of secondary inoculum, dissemination of sporangia, and infection of new host plant tissue. Viable inoculum persists in infected, unharvested cacao pods for at least a year, and each pod can develop at least four million sporangia within days of a rainfall event (47, 76).

Resistance is often difficult to find among existing varieties and incorporate into breeding lines, as many tropical tree crops have been domesticated from very limited germplasm diversity. For example, the Asian oil palm industry was based on four palms, believed to have originated from only one plant, introduced to the Bogor Botanic Gardens by the Dutch in 1880 (55). Most of the world's cacao and rubber trees found in modern plantations descend from a few individual trees obtained during only a few collecting expeditions (24, 111). Germplasm collections of tropical tree fruits, essential because seeds are short-lived and the germplasm has to be maintained as living trees, are also rather scarce and poorly resourced.

Many crops are grown as perennial monocultures over large areas to meet market demands. Bananas grown for export in Central America and parts of Asia are grown as large-scale monocultures of the Cavendish variety that are susceptible to Black leaf streak (a.k.a. Black Sigatoka) caused by *Mycosphaerella fijiensis* (91). Control requires frequent sprays of curative and protective fungicides, up to 70 times a year in some places (31). In some regions, as much as 25% of the cost of production consists of the control of this disease alone (100, 115). These monocultures are also prone to significant problems with soilborne diseases such as Panama wilt caused by *Fusarium oxysporum* f. sp. *cubense* (100, 119).

The deployment of successful disease management programs is often limited by the availability of relevant and accessible research data, extension services, and farmer capacity. Much of the early colonial research on plantation crops was published informally and collections have often been lost or require lengthy searches of archives. In most countries, research into tropical tree crops has declined in postcolonial times as national governments focus on other priorities. However, the benefits of much of this investment have failed to materialize, as productivity and income from tree crops, still a significant component of smallholder and national incomes, have not increased (110). Without higher agricultural incomes, farmers and governments are unable to invest in better education, health, and infrastructure. A pernicious cycle develops in which poorly educated, unhealthy farmers are limited in their capacity to resource and implement effective crop management (60).

IMPACT OF PLANT PATHOGENS IN TROPICAL TREE FRUIT CROPS

With high rainfall and abundant solar energy in the lowland wet tropics, it might be thought that agriculture should be highly productive. Unfortunately, this is seldom the case. Overall, it has been estimated that crop losses in the tropics are double those in the temperate zones (61, 131). In addition to pests and diseases, tropical soils lose their fertility rapidly once the rainforest leaf litter has been removed (110). Considering that 60% of the globe's arable land is located between the Tropics of Capricorn and Cancer, and that this is also where the human population is increasing fastest and poverty is most common, reducing yield losses caused by plant pathogens is paramount (131).

Unlike most temperate food crops, the actual yield potential for almost all tropical fruit crops remains unclear. Although some industrialized crops, such as bananas, citrus, and oil palm, have very high production efficiencies, this is more the exception than the norm. For most tropical tree crops, average yields over large areas are much lower than the maximum recorded yields. The gap between maximum attainable cacao yields (>8 metric tons/ha) under perfect conditions, and even those achieved routinely on experiment stations (3.5–4 metric tons/ha under ideal conditions), is in stark contrast to the average yields obtained by most growers (300–400 kg/ha) (67). The reasons for this yield gap include pests and diseases, poor soil and water management, low commodity prices, markets that fail to provide an incentive to growers, and a shortage of skilled and productive labor needed for improved management because of poor community health and nutrition (60).

We need to ask whether we know enough about diseases on tropical tree crops to effectively manage them. Holliday (63), among others, noted that the wholly unsatisfactory imbalance in our knowledge of plant diseases in the tropics resulted from the proportionately lower investment in plant pathology (124). Plant pathologists have long been fascinated by the highly specific interactions between pathogens and (usually annual) plants and have made great progress since Flor first postulated the gene-for-gene interaction (40, 41). Although resistance, avirulence, and effector genes have been cloned from temperate crop pathogens, and their interactions studied in great detail (30), destructive tropical pathogens with broad host ranges, such as *P. palmivora* or perennial *F. oxysporum* f. sp. *cubense*, remain poorly understood.

ARE THERE JUST MORE PATHOGENS IN THE TROPICS?

A global estimate of 1.5 million fungal species in 1991 (57) has recently been updated to "at least 1.5, but probably as many as 3 million" (58, p. 2,430), whereas other studies have put forward estimates as high as 3.5 million (86). All estimates are much larger than the 80,000 currently described fungal species (58).

Although the total number of fungi may be uncertain, their global distribution is more relevant. Plants in general conform to the latitudinal diversity gradient (LDG) (62), which predicts higher biodiversity in the tropics than in the temperate zones. Although tropical forests represent only 7% of the earth's surface, they contain more than half of the world's biota (139). We know that there are approximately 300,000 species of vascular plants and that the majority of them evolved in the tropics, where the proximity of different ecoclines provides ample opportunity for phytobiome diversity. It has been noted that the density and diversity of host plants in tropical lowlands may in part be due to high disease and pest pressure driving the rapid evolution of plants (54, 79).

Although the vast majority of research in plant pathology and mycology is conducted, and a large number of plant pathogens were first identified and described, in temperate zones, there is evidence that the LDG also generically applies to microbes. Wellman (136) concluded that for every disease that occurred in a given crop in the temperate zone, there were 10 in the tropics. It has also been estimated that there may be around 270,000 species of plant-pathogenic fungi in the tropics (113).

An additional issue of relevance to the tropics is the much higher abundance of insects (85) and therefore potential vectors of plant diseases such as viruses, viroids, and phytoplasmas (46). In addition, recent examples have shown that mollusks, tent-building ants, flying beetles such as the scolytids and nitidulids, and bush crickets such as Tettigoniidae act as agents of dispersal from

Figure 1

Mummified cacao pod showing insect holes. The pod was unharvested because it was infected with *Phytophthora palmivora*, which survives for up to a year. The insects, scolytids and nitidulids, act as passive vectors of the pathogen.

the ground into the canopy for *Phytophthora* species, which were typically not considered as being disseminated by insect vectors (**Figure 1**) (35, 70, 132).

We also need to consider that many tropical countries do not have the same resources and infrastructure as developed countries to detect and identify plant pathogens. It has been shown that total wealth of a country correlates with scientific and technical capacity and is the strongest predictor for observed pest numbers (43). National wealth also increases with latitude (71). Together, these lead to a lower observational capacity in the tropics compared with the temperate zones (8). Although the number of potential fungal plant pathogens for any given host plant can be disputed, it should be clear that the tropics harbor a large reservoir of known, emerging, and as yet unknown infectious plant diseases.

THE EVER-INCREASING SPREAD AND EMERGENCE OF INFECTIOUS PLANT PATHOGENS

Many fungi have originally inhabited spatially restricted endemic ranges (34), and during the first part of the Columbian Exchange humans utilized this advantage to grow crops introduced from other continents in the absence of serious pests and diseases, resulting in a yield honeymoon (28). However, in the current era of globalization, human-mediated intercontinental dispersal of fungal pathogens has increased dramatically (9, 38, 65). Our phytopathology journals over the past few decades contain ever-increasing numbers of reports of pathogens extending their ranges and of new and emerging infectious plant diseases (4, 78, 127).

In addition to new pathogens, a constant risk to crops around the world is the emergence and migration of new strains of known pathogens capable of overcoming resistance (116). The intercontinental movement of infected plant material partially explains the appearance of new emerging plant diseases in unexpected places. However, novel species and strains also arise as a result of sexual recombination, hybridization, and rapid evolution of introduced species under episodic selection pressures (18). Hybrid progeny may possess equal or greater virulence than parent species, thereby posing an increasing risk to our natural environment and agricultural production systems, as shown for *Phytophthora*, *Ophiostoma*, and other pathogens (11, 12). Horizontal transfer of genes encoding virulence factors, first demonstrated by Friesen et al. (42), has also contributed to rapid evolution in *Fusarium* and other species (103, 128).

Recent increases in fungal disease outbreaks are attributable to the many-fold increase in the trade of cryptically infected products and food (13, 66, 137). Genetic uniformity, especially of plantation crops, and bananas in particular, adds to the risk presented by emerging diseases. Minor pathogens in nature become epidemics in monocultures, such as South American leaf blight of rubber (72) and Fusarium wilt of bananas (99).

Spread of Cacao and Cacao Diseases

Cacao (*Theobroma cacao* L.) is native to Western Amazonia, where it occurs as a forest understory tree. The genus is thought to have evolved at the time of the Andes uplift, which separated distinct populations at the same time as joining Gondwanan and Laurasian landmasses and species, generating a rich diversification of plants, animals, and their associated microbiota (105). Cacao was domesticated at least 3,000 years ago, not for chocolate but for its sweet pulp and for medicinal purposes (20, 133), and spread to Central America and Mexico along a number of different trade routes (111).

Most of the world's commercial cacao comes from only a few prospecting expeditions, and it remains more a domesticated wild species than a cultivated species. Of the 10 genetic clusters of *T. cacao* identified (83), three are commonly recognized: *criollo*, *forastero*, and *trinitario* (117). *Criollo* types have pale beans and are the most sought after, as they produce the highest quality chocolate; however, they are low yielding and highly susceptible to several diseases. *Forastero*, a mixed group of Amazonian types producing purple beans, dominate global cacao production due to their robustness and high fruit yield. *Trinitario* is a natural hybrid of *criollo* and *forastero* that survived the blast (perhaps a hurricane, perhaps an epidemic) that destroyed *criollo* cocoa in Trinidad in 1727 (84). *Trinitario* combines the high quality of *criollo* with the robustness of *forastero*, and produces fine flavor cacao.

The Spanish transported *criollo* cacao from Mexico to the Philippines in 1670, where it spread across the Pacific, and the Portuguese took *amelonado* cacao (a type of *forastero*) from Brazil to West Africa in 1822. By the mid-twentieth century, Africa had become the major producer of quality cacao and now produces 70% of global supply (**http://www.icco.org/about-us/international-cocoa-agreements/doc_download/240-production-latest-figures-from-the-quarterly-bulletin-of-cocoa-statistics.html**).

Cacao is another good example of a crop that escaped its coevolved pests and diseases as a result of the Columbian Exchange. The only familiar pathogens confronted were pan-tropical species of *Phytophthora* (most commonly *P. palmivora*) that together cause global yield losses of at least 20% and tree deaths of up to 10% annually (**Figures 1** and **2**) (48). If left unmanaged, pod rot can destroy entire crops because of the persistence of primary inoculum in soil and infected pod mummies, short generation time, and massive quantity of airborne and vector-borne secondary inoculum produced in warm, wet weather. It is unclear based on current information

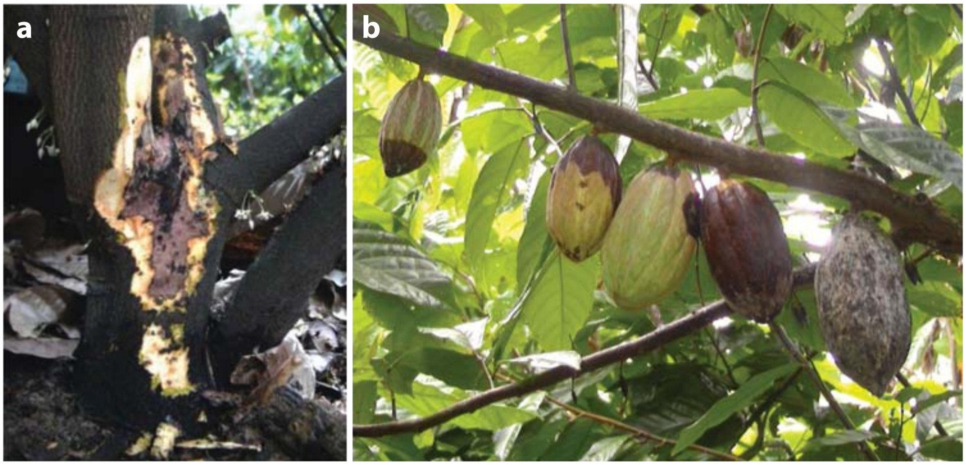

Figure 2

Phytophthora palmivora diseases of cacao: (*a*) trunk canker and (*b*) pod rot.

whether *P. palmivora* is native to South America, as postulated by Zentmyer (140), or Southeast Asia (75). In South America, *Phytophthora capsici* and *Phytophthora citrophthora* are also reported as minor pod rot pathogens, whereas *Phytophthora megakarya* leapt from native tree hosts in Africa to cacao and is now the major pathogen in parts of West Africa because it produces sporangia more rapidly on infected pods, precipitating even more explosive epidemics than *P. palmivora* (1).

Vascular-streak dieback (VSD) (**Figure 3**) was first described in the 1960s in Papua New Guinea as a progressive vascular wilt, initiating from shoot tips, causing defoliation and the eventual death of highly susceptible genotypes such as *amelonado* (68). Although its obligately parasitic habit prevents the completion of Koch's postulates, the pathogen is known to be *Ceratobasidium* (*Oncobasidium*) *theobromae*, and the disease is widespread across Melanesia and Southeast Asia (49). However, mystery still surrounds the biology of this newly encountered pathogen. The putative inoculum, basidiospores, is produced only on cacao leaf scars under continuous wet weather and remains viable for only a short time around dawn. Thus, isolated stands of cacao planted in newly cleared forest must be infected by airborne spores released from a nearby, but as yet unidentified host (109). Identification of this indigenous host would facilitate VSD management. However the disease can be effectively managed using a combination of quarantine and good nursery hygiene as well as by planting less susceptible genotypes and regular pruning and sanitation (49).

In contrast to VSD, two other destructive basidiomycete pathogens, Witches' broom (**Figure 4**) (*Crinipellis perniciosa*) and frosty pod rot (**Figure 5**) (*Crinipellis roreri*), coevolved with cacao in the Amazon basin, but both became epidemic when cacao trees were grown in high-density plantings (6). Neither disease has yet spread beyond South and Central America. Witches' broom destroyed the cacao industry in Surinam and Guyana around the turn of the twentieth century and spread to Ecuador (1921), the Caribbean (1928), and eventually Panama (1989). The introduction of Witches' broom in Bahia in 1989 is one of the few documented cases of bioterrorism and led to annual cacao production in Brazil dropping from 350,000 metric tons to 100,000 metric tons within 10 years (93), and the disease now accounts for approximately 20% of global disease losses.

Figure 3

Vascular-streak dieback of cacao. (*a*) Leaf necrosis and dieback (used with permission from Peter McMahon). (*b*) Vascular browning in infected stem (*lower*) compared with healthy stem (*upper*). (*c*) Necrotic vascular traces on leaf scars. (*d*) Sporophores.

Basidiocarps of *C. perniciosa* form on infected stems or pods and release the infective, airborne basidiospores for 2–8 days during alternating wet and dry conditions. In the presence of free water, basidiospores infect actively growing shoots, flowers, and young pods, causing hyperplasia (the characteristic Witches' broom), uneven pod ripening, and watery pod rot. Basidiospores are capable of long-distance dispersal in wind and water, with a range of up to 150 km reported; however, anthropogenic transport of basidiocarps, infected seed, and budwood presents a much greater risk. Some genetic resistance is available, although not necessarily durable, and sanitary pruning combined with applications of *Trichoderma stromaticum* (Trichovab®) remains the most effective, although labor-intensive, disease management tool (39).

Figure 4

Witches' broom (*Crinipellis perniciosa*) symptoms on cacao.

Figure 5

Frosty pod rot (*Crinipellis roreri*) of cacao. Note pink basidiocarps of *Crinipellis perniciosa* in the upper left. Used with permission of Dr. Lyndel W. Meinhardt, USDA/ARS Sustainable Perennial Crops Lab, Beltsville, MD, 20705-2350.

Frosty pod rot originated on *Theobroma gileri* in the submontane forests of Ecuador and Colombia, and spread to cacao in Colombia (1851), Ecuador (late nineteenth century), Venezuela (1940s), Panama (1950s), Costa Rica (1978), Peru (1989), Nicaragua (1991), and Honduras and Guatemala (1998) (36). The appearance of frosty pod rot led to rapid production losses of at least 50% and the abandonment of cacao farming in many affected areas. Frosty pod rot currently accounts for approximately 5% of global disease losses but poses a much greater threat should it be introduced to Africa or Asia (39). Like *C. perniciosa*, *C. roreri* infects actively growing young pods, but after 1–3 months develops a white fungal mat bearing masses of powdery spores on the pod surface (39). The threat to global cacao production results from a number of features of the pathogen biology: The powdery spores are produced in enormous numbers over several months, readily dispersed by wind, water, and humans, and extremely robust. Considerable debate continues on the nature of these spores, with some authors describing them as modified meiospores (37), while others conclude they are conidia (32). Strict quarantine precautions are in place to minimize the risk of further spread of the disease; sanitary pruning and regular harvesting are labor intensive but remain the most effective control methods (39).

Other minor pathogens are locally important but potentially threatening should they emerge in new environments, include *Ceratocystis* wilt (mal de machete) and *Rosellinia* black root rot and pink disease (*Erythricium salmonicolor*) (97).

Spread of Banana and Banana Diseases

Bananas were moved from their center of diversity, temporarily leaving behind most of their coevolved pathogens. However, as with other crops, bananas must endure a range of newly encountered diseases when grown in new areas. Most cultivated bananas are triploid and can trace their origin to the diploid *Musa accuminata* (AA) species, whereas other cultivated bananas are derived from crosses between *M. accuminata* and *Musa balbisiana*, which supplies the B genome (114). It is hypothesized that only *M. accuminata* was domesticated in Southeast Asia and that its cultivation spread north to overlap with the *M. balbisiana* range, creating opportunities for spontaneous hybridization and the creation of triploid hybrids showing increased vigor and yield (114). Banana cultivation spread from Southeast Asia via Madagascar to Africa around the year 300 (29). Bananas were introduced into the Canary Islands by the Portuguese around 1500 and from there were brought to the New World by the Spanish in 1516 (69). It was only when refrigerated shipping and artificial ripening became available that an export market started in the Americas using a single variety, Gros Michel, that was thick skinned and could withstand long-distance transport. The early history of bananas in the Americas was one with relatively few disease problems until the early part of the 20st century, when Panama wilt spread from its ancestral home in Asia to Central America and destroyed vast plantations of the susceptible Gros Michel plantings.

Panama wilt. Fusarium wilt of banana, also called Panama disease, caused *by F. oxysporum* f. sp. *cubense*, is an example of a coevolved soilborne pathogen spread around the globe by humans. Fusarium wilt is believed to have originated in the Indo-Malayan region (101), and several different races of this fungus have been recognized. Race 1 affects common varieties such as Gros Michel, Lady Finger, Silk, and Ducasse; Race 2 affects Bluggoe; and Race 4 affects Race 1 and 2 susceptible cultivars as well as those in the Cavendish subgroup. Race 4 is further subdivided into subtropical and tropical variants: subtropical race 4, which can only attack Cavendish varieties in the presence of other stresses such as cold, and tropical race 4 (**Figure 6**), respectively (96). Race 3 is only pathogenic on *Heliconia* spp. (100).

Figure 6

(*a*) Symptoms of Fusarium wilt tropical Race 4 in Cavendish bananas. (*b*) Internal symptoms of vascular tissue in the pseudostem. (*c*,*d*) Cut section showing internal symptoms inside the pseudostem.

Fusarium wilt of bananas was first reported in Australia in 1874 (7), and Bancroft also noted that sugar and ladyfinger bananas were highly susceptible to this disease, whereas dwarf Cavendish was resistant. In 1890, this disease was first noticed in Panama in Central America in export plantations with the variety Gros Michel. From Panama, human-assisted spread of the pathogen to other parts of Central and South America occurred rapidly (95, 119). Panama wilt Race 1 also spread to other parts of the world outside Asia and was identified in West Africa in 1924 (119) and East Africa in the 1950s (10, 119).

The introduction of Panama wilt to Central America in an industry reliant on a single, highly susceptible variety had a major impact. New plantations were established but also became infected through the planting of visibly healthy but infected vegetative planting material. A significant amount of research was undertaken on the epidemiology (106), survival in soil (118), infection

(16) and pathogenicity (118, 122, 123), and many large-scale field trials were conducted in an effort to manage the disease (119). However, the epidemic swept through Central America's banana export industry and gave rise to the replacement of Gros Michel for the export market with clones of the resistant Cavendish in the 1960s (16).

Following the introduction of Cavendish, much research on *Fusarium* biology, epidemiology, and management in banana plantations was reduced. Although nothing pleases plant pathologists and plantation owners more than a forgotten disease, we usually find that victory is fleeting. Although there were numerous reports that the resistance was vulnerable (95), the march of Cavendish continued. Reports of strains in Southeast Asia that were highly aggressive on Cavendish cultivars in the absence of environmental stress were largely ignored (80, 125, 126). Lack of awareness and vigilance allowed the movement of infected planting material that gave rise to the spread of the new TR4 strain from Taiwan to Southern China, the Philippines, Malaysia, and Australia. More recently, an alarming increase in the intercontinental spread of TR4 has taken place, as the pathogen has now been found in the Middle East, including Jordan, (44), Lebanon (89), Oman (unconfirmed), and Pakistan (89). Recently, the pathogen has also been identified on the African continent, causing major problems in Mozambique (90).

It is concerning to note that although we know a lot more about TR4 than we did about Race 1 when it first appeared more than a century ago, the current spread of TR4 around the globe is much quicker than the spread of Race 1, which took place over several decades. There are several reasons for this increase in the rate of spread, including mechanization, which is responsible for movement of contaminated soil between farms and increased surface water irrigation. Despite the presence of clean planting schemes involving tissue culture, bits and suckers are still used in some areas. The other main issue and the reason for intercontinental spread is the massive increase in the movement of humans and materials around the globe.

Black Sigatoka. Black Sigatoka, caused by *M. fijiensis*, and Yellow Sigatoka, caused by *Mycosphaerella musicola* (77), are major leaf diseases on banana (91) (**Figure 7**). Although disease was first noticed in the Sigatoka district of Fiji in 1963 (104), it may have originated in the New Guinea–Solomons Islands area (120). From there, it spread to West Africa (102), Southern China (115), and East Africa (26), and is now well established in most areas on the African continent where bananas are grown (19). Black Sigatoka was first detected in the Americas when it was identified in Honduras in 1972 (121). It not only attacked export cultivars in the Cavendish subgroup, but it also was pathogenic on cultivars of the plantain subgroup (AAB) when grown in coastal lowlands. From its initial introduction in Honduras, it spread rapidly and has now reached almost all banana and plantain production regions on the continent (108). Australia is the only continent where bananas are grown that is free from Black Sigatoka, although there have been numerous incursions that have all been successfully eradicated (59).

In many areas planted with Cavendish cultivars, Black Sigatoka has replaced Yellow Sigatoka as the main leaf disease. However, this is not the case in many countries where other cultivars dominate, such as many parts of Indonesia, Thailand, and Brazil. In these countries, both Yellow and Black Sigatoka can be found at varying proportions, depending on prevailing environmental conditions and types and cultivars grown (73).

The main difference between Black Sigatoka and *Fusarium* is in their mode of spread. Black Sigatoka relies on the aerial dispersal of conidia and ascospores for local and regional spread, and humans for intercontinental spread. *Fusarium* is a soilborne disease that naturally spreads very slowly through the movement of infested soil and water over relatively short distances. Long distance is human assisted through infested plant material and soil attached to equipment and shoes.

Figure 7

Black Sigatoka in banana.

HOW DO WE MANAGE TROPICAL FRUIT TREE DISEASES?

There are many reasons why control of plant diseases on perennial fruit crops in the tropics is more challenging than in temperate zones. It has been said that "the management of diseases of tropical perennials is one of the greatest challenges in production agriculture" (98, p. 660). Below, we outline some of the options for disease control.

Exclusion of Pathogens

Exclusion is the most cost-effective way to control plant diseases but requires a proactive approach involving apparent restrictions on trade, awareness by growers and the general public at large, detailed information about the distribution and dissemination pathways of pathogens, and an effective quarantine strategy operating on sound principles of plant pathology. Regionally important diseases such as VSD, Witches' broom, frosty pod rot, and *P. megakarya* on cacao pose a major threat to the global chocolate industry, and all germplasm exchanged for breeding programs must first pass through the International Cocoa Quarantine Center in the United Kingdom. However, the Catch 22 funding situation, where resources are mostly allocated for research on well-established diseases of economic importance, with little, if any, going to emerging diseases, prevails. Allocating resources to work on prevention and containment of exotic and emerging diseases is supported by presenting the exclusion benefits to policymakers and funding organizations. For example, in Australia, the exclusion benefits for several plant diseases of banana, such as *Banana bunchy top virus*, Panama wilt, and Black Sigatoka, have been quantified in great detail (21–23), and fighting exotic pests and diseases is as important as battling endemic diseases. Although exclusion of pathogens is economically highly rewarding, the reality is that biosecurity is not foolproof and it is paramount that we anticipate the eventual arrival of pathogens and start preemptive breeding and management strategies.

Clean Planting Material

Exclusion of pathogens can take place at different geographic scales, from intercontinental to local fields. In all cases, it is important that the material we use for planting be free from pathogens. In order to achieve this, many countries have clean planting schemes in which material used for planting is obtained from mother plants of a high health status that are tested for the absence of pathogens. In intensive crops like banana, virus-free, meristem-derived plantlets are often used, and tissue culture has an additional advantage: As it is soil free, it prevents the movement of pathogens such as *Fusarium*. However, asymptomatic planting material poses a significant risk in many tropical tree crops, as the use of serological or molecular-based diagnostics to test planting material is often lacking because of underinvestment in research and capacity development.

Similarly, poor nursery practice is a common source of infected planting material, as nursery managers seek to cut costs. Using infected field soils as potting mix, contaminated irrigation water, and poor nursery drainage all contribute to high losses due to soilborne pathogens such as *Phytophthora* and *Pythium*, and attempts to control these diseases using systemic fungistats compound the problem, as these usually only suppress symptom development in infected planting material (112). Although improved nursery practices provide compelling returns on investment (27), they require training, finance, and labor, resources that are often limited in tropical countries. Furthermore, farmers need to be convinced of the long-term benefits of purchasing certified disease-free planting material when they face short-term financial constraints.

Germplasm Improvement

Large-scale monoculture is the norm in industrialized crops like bananas, oil palm, and rubber. Furthermore, many tropical tree crop industries have been founded on domesticated wild species using only a very limited amount of genetic diversity. It is remarkable how little of the world's plant diversity we actually use to produce our food. Even for annual crops, we utilize little genetic diversity, and it has been estimated that only approximately 5% of the genetic variability present in *Solanum* is found in the potatoes now grown around the world (130). For tropical crops such as bananas and cacao, this is significantly lower. There are several reasons for this, including high cost of replacing varieties in the field, time scale of progress, capital requirements, processing standards, market preferences, and absence of innovation in the supply chain. In major tropical tree crops such as banana and cacao, the effort in breeding is miniscule compared with the global importance of these crops. The focus of many breeding programs for tropical fruit crops is also questionable, as they heavily concentrate on potential yield in the absence of pests and diseases and in the presence of agrochemical inputs such as fertilizers and pesticides on research stations, and ignore performance in the field under smallholder conditions where these inputs are applied at a lower level, if at all. This yield gap impacts even the best farmers of annual crops but to a smaller degree than smallholders growing perennial tree crops in the tropics (87, 88).

In the case of cacao, there is an enormous yield gap, and pests and diseases are often dismissed as externalities to be managed using pesticides. The lack of incentives for breeding has also resulted in limited collection and inventarization of germplasm. Owing to the growing world population, especially in the tropics, and deforestation in the centers of origin of tropical tree crops, the available biodiversity in the tropics is eroding rapidly. A long-term outlook in which we use a large percentage of the available diversity and efforts to collect and characterize the available germplasm for valuable traits and pest and disease resistance combined with preemptive breeding for major emerging diseases is needed. An excellent example of what can be achieved with such an approach is the development of a large number of multilines of coffee under the variety name Colombia and later Castillo, which have multiple vertical and horizontal genes for resistance to coffee rust in Colombia (2, 82). It is interesting to note that this breeding program was started prior to coffee rust being present in Colombia. The benefits of this approach are now being enjoyed by more than two million people involved in coffee production in Colombia (5).

Cultural Control

Basic agronomy, microenvironmental manipulation, and reduction of inoculum are important parts of integrated disease management strategies in tree crops. Cacao yields increased several-fold following the implementation of sanitation, regular and complete harvesting of pods, canopy and weed management by stimulating flowering, and reduction of *Phytophthora* pod rot through removing primary inoculum and the production and dissemination of secondary inoculum (50). Similarly, the improvement of drainage and good sanitation effectively controls *Phytophthora* root diseases of citrus, durian, and jackfruit (27).

Early diagnosis of disease is important to prevent further spread. In bananas, plants showing symptoms of *Banana bunchy top virus* need to be removed in a timely manner and an insecticide applied to knock down aphids, which potentially carry the virus, to control this disease. Panama wilt is controlled through early diagnosis and in situ destruction of the plants through an injection of glyphosate to prevent further buildup of inoculum and spread of the pathogen.

Biological Control

There are few examples of effective inundative biological control of fungal diseases on tree crops in the tropics. The fundamentals of *Phytophthora* epidemics that rapidly propagate and disseminate vast numbers of infective propagules under conducive environmental conditions make small reductions in primary inoculum through biocontrol agents inconsequential in the tropics.

More promising approaches aim to reduce the persistence of primary inoculum, such as the use of *Trichoderma* to parasitize sporocarps of Witches' broom disease of cacao (39). Increasing soil organic matter enhances soil microbial activity and suppresses pathogens, and, as a component of an integrated disease management strategy, contributes to productivity improvements in conjunction with improving soil drainage, root vigor, and plant nutrition.

Chemical Control

Large plantation owners in the tropics use modern chemical approaches to combat fungal diseases such as the aerial application of protective and systemic fungicides, for example, to control Black Sigatoka in bananas. However, the ready access to effective agrochemicals and supply chain demand for uniform Cavendish bananas has stifled the search for bananas with higher levels of resistance to leaf diseases in most regions. The exception to this is Cuba, where FHIA hybrids with much higher levels of disease resistance to Black Sigatoka and lower inputs of fungicides have been successfully applied (94).

Smallholders, however, often do not have access to appropriate chemicals and lack the information, capital, and equipment to apply fungicides in a safe and effective manner. Although they have smaller, usually mixed, holdings, a large proportion of small holders in an area grow the same crops so that escape from disease is not commonly observed; however, in most cases the incidence may be lower. This is countered by generally poorer crop management, resulting in much higher disease losses in smallholder plots. This is further exacerbated by a poor understanding of pathogen biology, infection, and disease cycles, leading to the use of inappropriate fungicides and incorrect rates and timing of application. Disease pressure is often highest in the wet season, when the application of fungicides is least effective. The application of fungicides with a single mode of action is thus placed under enormous pressure, and high pathogen populations develop fungicide resistance rapidly (74).

Another major problem in many tropical countries is the lack of expert independent information concerning the choice and timing of agrochemicals. Rigorous field testing and validation of chemicals are rarely done under regional conditions, and unfortunately one often encounters a product-driven rather than solution-driven approach to the control of plant diseases. Other issues to consider involve human health during application of products as well as chemical residues in harvested fruit.

LESSONS LEARNED AND CHALLENGES AHEAD

The impact of diseases in tropical fruit tree crops is not well quantified, but the large yield gap provides a glimpse into the scale of the problem. Knowing the size of the impact of diseases on the tropical fruit crops through crop loss assessment would be helpful in efforts to allocate more resources to this area. It should also be clear that the disease problems are growing because of increased travel and trade within and between tropical countries, where the majority of biodiversity for fungal pathogens already exists. Increased trade between Central and South America, Southeast Asia, and Africa will further accelerate the human-mediated intercontinental dispersal of known and emerging infectious plant diseases, especially as biosecurity capacity is limited and underfunded. The challenge is especially large considering the potential number of fungal plant pathogens present in the tropics (113, 136).

Outside of a few major pathogens, especially in the tropics, we are not systematically tracking the global distribution of plant pathogens (8). Sound information upon which to base judgments on the potential of emerging infectious diseases is generally lacking. In depth knowledge of the etiology and epidemiology of many tropical plant pathogens is lacking. Quarantines need to be strengthened on a worldwide basis to counter the increased spread and dissemination of emerging infectious diseases. However, owing to limited national and regional phytosanitary capacity and the impetus to remove trade barriers, tropical countries are vulnerable to emerging infectious plant diseases (135).

The Green Revolution in agriculture focused closely on carbohydrate security. We now need major advancements in horticulture in the tropics that focus on nutrient security (60). In addition to the availability of nutrients at a regional level, horticultural crops of high value are also very important for economic development in the tropics. Tree crops drive economic development because higher value products enable the generation of incomes to pay for schooling and health care. The challenge ahead is large but not new, as attested by Thurston (130, p. 244): "Agricultural research alone cannot solve the problem of world hunger, but hunger cannot be significantly diminished without greatly expanding agricultural research." There is a need for long-term support for these tropical tree fruit crops in the face of complacency following the Green Revolution and government focus on rice and wheat for food security.

TRAINING

Training plant pathologists who can solve problems in the tropics is essential. Although the developed world trains many young scientists from developing countries, the question needs to be asked whether there is a knowledge gap in applied plant pathology in the tropics. Scholarship schemes train many students from the tropics in modern laboratories in developed countries, but in most cases the training and education relate to well-funded and highly technical research into temperate disease problems. In addition, students from the tropics trained in developed countries often lack a career path when they return to the tropics. Many find themselves returning to administrative rather than technical roles because of their newly acquired qualifications.

The tropical plant pathologist needs a much broader education, as their work more often focuses on dealing with the practical aspects of diagnosing and managing major plant disease problems, rather than an academic study of the underlying causes of disease. In addition to a lack of broad knowledge about pathogen biology and disease control, regional knowledge of diseases and their control is often inadequate, and advisory services and capacity are under-resourced or even nonexistent. Thus, solutions for plant disease problems that have been implemented elsewhere in the world are not adopted or implemented in many parts of the tropical world.

Hence, the challenges for a young pathologist in the tropics are extensive, and resources are rarely available to enable even the most dedicated to make a significant difference in crop productivity in their local area. In general, there is a lack of access to specific courses and resource materials for tropical plant pathology. In the current era of the Internet, we should be able to provide more relevant and accessible web- and mobile-based resources. In addition to hands-on training in the field of plant pathology, it is also important that students become familiar with tropical crops and farming, as there is no classroom substitute for practical farm experience (129).

Western scientists are often confused and frustrated by the limited adoption of new practices and the slight yield increase obtained by farmers because they do not appreciate the collateral constraints faced by smallholder farmers in the tropics (130). Understanding smallholder farming in the tropics in a broader sense includes understanding language, culture, customs, variability, instability, low commodity prices, market transparency, infrastructure, labor, and community health. Although these topics are beyond the scope of plant pathology, their relevance to technology adoption argues strongly for a more holistic, interdisciplinary approach to farmer training.

FUNDING FOR RESEARCH

We have highlighted that research funding usually becomes available only after a catastrophe has happened. A long-standing challenge for plant pathologists is that we need to convince financially constrained administrators and governments of the need to prioritize precautionary research and education on emerging infectious diseases before the diseases are introduced. Irrespective of the pathogen, it is paramount that we spend more time, effort, and resources on limiting the spread of emerging infectious diseases and that we try to avoid the trap in which funding is only provided for work on existing diseases. Black Sigatoka and Panama wilt are just two excellent examples in which resources became available for research only after pathogens were reported in a country.

Improving the management of many plant diseases of tropical tree fruit crops requires a long-term commitment to research, as farm-level impacts generally take at least a decade. Short-term funding rounds of 3–5 years are inefficient and expensive relative to sustaining the flow of investments into recurring crop health problems and building capacity. We should keep in mind that research on plant pathogens is relatively cheap until it is ignored, and we have to deal with the much more expensive consequences.

CONCLUDING REMARKS

Plant disease causes significant losses to production in tropical horticulture, and reducing these losses results in more effective and sustainable food production and income generation, particularly in developing economies (110). In this review, we have outlined some of the challenges pathogens present to tree crops in the tropics. We have also identified the particular challenges presented in tropical perennial crops, using bananas and cacao as examples, and put forward some strategies that may help reduce disease impacts and thus the yield gap. The common themes that have emerged include improving our understanding of pathogen, crop, and disease biology, strengthening diagnostic and quarantine capacity, utilizing germplasm, screening for resistance, focusing on the relevance of training and research programs, and appreciating the environmental, social, and economic context of plant disease.

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