Chapter 1 Potatoes, Citrus and Coffee Under Threat



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Abstract Four familiar breakfast foods, coffee, oranges, bananas and potatoes provide current examples of the challenge to food security posed by plant diseases. Potato late blight, a disease with a historical link to famine and a continued threat to a staple crop; huanglongbing, a devastating disease that threatens the citrus industry; coffee leaf rust, a disease that compromises a commodity and the livelihoods of those who service it; and Fusarium wilt of bananas, a globally damaging disease with a virulent race that is currently spreading. What if these morning staples were to become scarce or unavailable? This chapter reflects the discussions of an expert panel at a public meeting, held as part of the 2018 international Congress of Plant Pathology at Harvard Museum of Science and Culture. The focus of the panel that included specialists in plant pathology and in food security, is on emerging diseases, covering topics that include the evolution of plant pathogens, tracking how they spread around the globe, and strategies to combat plant diseases that are threatening global food security.

Introduction

Coffee, oranges, bananas and potatoes are among the most widely consumed breakfast foods. What if these morning staples were to become scarce or unavailable? In this opening section of the book we focus on familiar foods to provide current examples of the challenge to food security posed by plant diseases.

At the 2018 International Congress of Plant Pathology, in Boston MA, an expert panel was convened in a packed evening session open to the public at Harvard Museum of Science and Culture to consider the impact of four such diseases that currently present severe threats to food security (Fig. 1.1).

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Fig. 1.1 The panel (left to right): Megan M. Dewdney, University of Florida; Randy C. Ploetz, University of Florida; Angela Records, USAID, Washington DC; Gary D. Foster, University of Bristol; and Jean B. Ristaino, NC State University

Potato blight¹

A disease with a historical link to famine and ongoing potential to threaten a staple crop

- Huanglongbing of citrus Megan M. Dewdney² Probably the most devastating citrus disease – it threatens an industry
- **Coffee leaf rust Angela Records and Jacques Avelino**³ A disease that compromises a commodity and the livelihoods of those who service it
- Fusarium wilt of banana Randy Ploetz

A globally damaging disease with a virulent race that is currently spreading.

To capture a flavour of this public event the book opens with an account of a crime scene, with evidence left by the Irish potato famine of what came to be recognized as an epidemic of a plant disease and its culprit – potato blight.

This is followed by brief overviews of two currently critical diseases of citrus and coffee – huanglongbing and leaf rust.

The next chapter tells the unfinished story of the advance of tropical race 4 of Fusarium wilt of banana.

¹The name "potato blight", or just "blight", is used informally in this chapter for the disease caused by *Phytophthora infestans*, responsible for the Irish potato famine. The disease is more formally known as "potato late blight", to distinguish it from "potato early blight", a different disease caused by *Alternaria solani*.

²Based on the panel presentation by Megan M. Dewdney, University of Florida, Lake Alfred, FL, USA.

³Based on the panel presentation by Angela Records, USAID, Washington, DC, USA and Jacques Avelino, CIRAD-CATIE-PROMECAFE, Coronado, Costa Rica.

Each of these diseases poses immediate threats not only to a crop but also to the livelihoods of hundreds of thousands of people involved in their cultivation and in food production. The focus of our panel – specialists in plant pathology and in food security – was on emerging diseases, covering topics that include the evolution of plant pathogens, tracking how they spread around the globe, and strategies to combat plant diseases that are threatening global food security.

Crime Scene Investigations: CSI Dublin – Tracking a Potato Killer

The Irish potato famine of the 1840s was the result of potato late blight, a serious disease of potatoes caused by the plant pathogen *Phytophthora infestans* (Fig. 1.2). The Irish famine was not only an issue of food security; it also threatened the national security of Ireland. The Irish working poor were highly dependent on potatoes as their staple food and when the crop failed, many people starved. The dependence on potatoes was remarkable: an adult male would consume 9–11 pounds of potatoes per day, with little diversity in diet. Though other crops such as oats and wheat were grown in Ireland in the nineteenth century they were largely exported to England. Only after the magnitude of the famine emerged was food aid increased to Ireland (Bourke 1993). The potato blight threatened both food security and Ireland's national security.



Fig. 1.2 Symptoms of blight caused by Phytophthora infestans on potato

When there was not enough food to go round and no surplus that could be sold to pay the rent, families were evicted from their homes. The Irish crime scene expanded as the potato crop failed. Many people moved into workhouses where human diseases were rife. A million Irish lives were lost during the potato famine through hunger and disease, especially among the poorest people. An additional two million left the country in mass emigration, often in unsuitable ships, with further loss of life. Conditions on these "coffin ships" and subsequent quarantine of the immigrants in places such as Grosse IIe in Quebec resulted in the spread of human diseases and thousands more perished *en route*. At a mass burial site in Grosse IIe, over 5000 Irish immigrants were buried after they died from disease.

The 2018 International Congress of Plant Pathology was held in Boston MA, where many of the surviving Irish emigrants settled. A monument to the Irish famine in Harvard Square declares "Never again should a people starve in a world of plenty" (Fig. 1.3). Regrettably, food security remains a huge problem in the twenty-first century, globally and in areas of the USA. Plant diseases continue to make a major contribution to the challenge of food security.



Fig. 1.3 Statue commemorating the Irish immigrants in Harvard Square, Boston

Naming the Culprit – Phytophthora, the "Plant Destroyer"

When the potato famine struck there was little understanding that pathogens cause disease. Who was the suspect in in this crime scene? The disease first occurred in 1843 in the USA. In 1845 it was reported in Europe and the British Isles. The 1843 Commissioner of Patents report (Ellsworth 1843) said, "The potato crop has been attacked. The cause is generally attributed to the peculiarity of the weather". Others claimed "It was certain that a fungus appeared in the leaves and tubers but it was uncertain how far the fungus was the cause or consequence of the disease" (Johnson 1845). Theories on the cause included bad air, the wrath of God, racial prejudice against the Irish, or a minute fungus (Fig. 1.4) (Ristaino et al. 2020). The British mycologist Miles Joseph Berkeley observed a characteristic microorganism on diseased potatoes, but was this the cause of the disease or an incidental result of some other cause (Berkeley 1846)? He published a detailed description of the disease, drew pictures of the pathogen and collected plant samples which remain in Kew Gardens Mycological Herbaria (Ristaino 1998). It was 30 years later in 1876 that Anton de Bary elucidated the full life cycle of the pathogen and, based on morphology of sporangia and sporangiophore characteristics, changed the pathogen name from Peronospora to Phytophthora infestans (De Bary 1876). The word *Phytophthora* means "plant destroyer". This work on a plant disease preceded work done by Louis Pasteur and Robert Koch on the germ theory of human disease.



Fig. 1.4 Sporangia of Phytophthora infestans on a tomato leaf

Charles Darwin

Charles Darwin studied and wrote about the pathogen after the disease struck his farm at Down House in England (Ristaino and Pfister 2016). Potatoes were the subject of some of Darwin's investigations, including studies of flowering and sexual reproduction. Darwin described the disease as a "painfully interesting subject" in letters to his cousin William Darwin Fox. Darwin had collected samples of wild potatoes from Chile during his voyages on HMS Beagle 10 years earlier, and those tubers were grow-out during the famine years to test for resistance to the disease. Unfortunately those tubers "fared exactly the same as the other kinds, having blotched in the leaf and a few tubers decayed' (Fox 1846). Darwin supported work by James Torbitt, an Irish merchant and potato breeder, from his personal funds in a search for resistance. Some of Darwin's heirloom potatoes are still grown at Down House and have potato blight.

The Spread of Potato Blight

The pathogen produces copious sporangia on leaves that can be carried by wind and rain over kilometers to spread the disease (Fig. 1.4). It is also dispersed in infected potato tubers. The blight epidemic began in 1843 in the USA, starting from the ports of New York and Philadelphia, and spread to a five-state area (Bourke 1964; Ellsworth 1843). The first appearance of the disease near the two port cities suggests an introduction via imported tubers. Two years later the disease was reported in the mainland of Europe and then spread across the English Channel into England and Ireland.

Research in my lab has focused on several "Big questions" including identifying the actual lineage that caused the famine and identifying where the pathogen came from, determining if the same lineage caused disease in the USA and Europe and Ireland, and comparing the genome to modern lineages (Martin et al. 2013; May and Ristaino 2004; Saville et al. 2016). We were the first to work with historic specimens from the actual famine era outbreaks (Fig. 1.5) (May and Ristaino 2004; Ristaino et al. 2001). Some of those specimens are housed in the Farlow Herbarium at Harvard University. We amplified three mitochondrial genes and, using SNPs from those mitochondrial genes, we were able to demonstrate that the Ia mtDNA haplotype was responsible for the first outbreaks and not the 1b haplotype as previously believed (May and Ristaino 2004; Ristaino et al. 2001; Ristaino and Hu 2009). The US-1 lineage was not the culprit behind the famine. The culprit was another SSR lineage altogether, which we subsequently named FAM-1 (Saville et al. 2016).

In 2007, The Broad Institute at the Massachusetts Institute of Technology in Boston and a large team of scientists sequenced the first full genome of *P. infestans* (Haas et al. 2009). The sequence shed light on the unusually large genome and revealed effector diversity in the pathogen. Effectors or avirulence proteins were





present in gene-sparse regions of the genome. The size of the genome suggested that genome expansion had occurred but further work was needed to understand that expansion. Advances in genome sequencing technology and reduced costs opened the possibility of sequencing the whole pathogen genome from historic herbarium specimens (Martin et al. 2013).

Collections from the Farlow Herbarium at Harvard, The Royal Botanic Gardens, Kew, UK, and the USDA National Fungus Collections were used in our research. The earliest samples known to be infected with *P. infestans* are housed in these important collections. Several questions of interest included whether the pathogen genome had always been large, and whether historic populations were asexual. In order to understand the evolutionary relationships among historic and more recent aggressive lineages and to determine where the famine lineage originated, comparisons of modern and historic genomes were done. We studied genome evolution with collaborators Tom Gilbert at the University of Copenhagen and Mike Martin (now at Norwegian University of Science and Technology) (Martin et al. 2013; Martin et al. 2016). At first, five historic genomes were sequenced and compared to modern-day lineages circulating in the US (US-22, US-23 and US-8) and Europe (3_A2) and the Broad sequenced strain (T30-4) (Martin et al. 2013). This study

corroborated our previous work (May and Ristaino 2004; Ristaino et al. 2001) concluding that the historic lineage was not the US-1. There was a highly supported monophyletic clade containing the historic lineages. The modern lineages were distinct and differed by over 120,000 SNPs, suggesting genome evolution and expansion with time. Many of the *Avr* genes known to be essential for virulence in modern *P. infestans* were absent in the historic lineages (Martin et al. 2013; Vleeshouwers et al. 2011) including some of the expanded set of pathogen effectors. Subsequently, we sequenced 45 additional mitochondrial genomes from historic and modern lineages (Martin et al. 2014) and results indicated that the HERB-1 (Ia) mtDNA lineage was present in Mexico and Ecuador, thus refuting the claim that the lineage was extinct (Yoshida et al. 2013). The divergence time of the HERB-1 mtDNA lineage was dated to 75 years prior to the Irish famine outbreaks (Martin et al. 2014).

We used 12-plex microsatellite analysis from a larger set of several hundred historic samples and identified the FAM-1 SSR lineage in nineteenth century USA and European samples. The same lineage caused disease on both sides of the Atlantic. Interestingly the FAM-1 lineage was found in the oldest South American samples, from Costa Rica and Colombia. The US-1 lineage was more prevalent in the midtwentieth century. The FAM-1 lineage was present for over 100 years with a widespread distribution over six continents.

Potato Blight Today

Potato blight is not just of historic significance; it continues to cause severe disease wherever potatoes are grown (Ristaino et al. 2020). The disease is particularly devastating for smallholder farmers who do not have access to fungicides or resistant varieties. One hundred and seventy-five years after the famine, we are still trying to manage the disease. We know the pathogen moves aerially but it also moves in infected tubers and plant material. The trade and movement of potato tubers is complex and seed networks of potato can be used to understand pathogen spread (Garrett et al. 2017). Seed tubers are not always certified when they move across borders. The pathogen's polycyclic life cycle also contributes to disease spread. We have identified mefenoxam-resistant lineages. The pathogen can also shift hosts, can infect wild Solanum and petunias, and thus can exploit multiple niches. We have found P. infestans in herbarium samples from the 1850s from petunia, suggesting that the pathogen exploited alternative hosts soon after it was first described. The pathogen genome is very plastic and effector diversity contributes to increased virulence of some strains. Monoculture of susceptible varieties also contributes to disease. There are resistant varieties available but they are rarely planted on an agricultural scale. Transgenic potatoes that have resistance to the disease have been developed by the International Potato Center but the hurdles in deploying transgenic plants in the developing world are still large (Ghislain et al. 2019). Even in the USA, transgenic potatoes are not widely grown.

In 2009, a blight pandemic occurred in the USA, caused by a single lineage of US 22 (Fry et al. 2015). The lineage was spread on infected tomato transplants produced

in the south and dispersed to the northeast. The disease went undetected until it had spread to many locations, first on backyard tomatoes and then in grower fields. A team funded by a USDA NIFA grant developed the USABlight disease alert and surveillance system (Fry et al. 2013). The surveillance system sends text alerts of disease outbreaks to help growers in timing their fungicide applications. Identification of pathogen genotypes is done using 12-plex microsatellite markers and a decision-support tool was developed that uses weather data to forecast when to apply fungicides (Liu et al. 2018; Small et al. 2015; Saville and Ristaino 2019). We are also developing innovative methods to diagnose the disease rapidly using LAMP assays (Ristaino et al. 2019). This technology will allow real-time diagnosis in the field using cell-phone-based diagnostic tools that identify the pathogen in a matter of minutes, and can create outbreak maps (Li et al. 2019; Paul et al. 2019; Ristaino et al. 2019).

A global surveillance system for late blight is needed. Monitoring is heavily focused on northern Europe and the USA. Other regions of the world including Latin America (LatinBlight), China (AsiaBlight) and Africa (AfriBlight) are now beginning to collect and organize datasets and to map disease outbreaks and lineages. Funding has been a limiting factor in developing and maintaining global surveillance databases and in linking partner countries for collaborative projects. We have developed a queryable database that will enable global populations to be genotyped and identified more easily.

The exploitation of potato biodiversity for development of disease-resistant potatoes needs further research. The potato biodiversity of the Andean region is an important source of host resistance, but there is a need for more study of the biodiversity of the host and of pathogen evolution in the field, to limit occurrence of resistance-breaking strains. Host resistance is the best means for smallholders to manage blight effectively.

Climate change is expected to influence the global spread of blight; some areas may become less conducive to disease as temperatures rise. Planting climateadapted potatoes with resistance to the disease is an important development. Continued monitoring of pathogen populations is needed to help limit disease spread and optimize management strategies, including the deployment of durable host resistance.

Huanglongbing: The Disease that Could Eliminate Orange Juice and Grapefruit from the Breakfast Table²

Probably the Most Devastating Citrus Disease Known

Citrus production around the world is slowly coming under threat from the disease called huanglongbing (HLB), a dialect name from China where it was first found in China, meaning yellow dragon disease (Blaustein et al. 2018). It is also called citrus greening. The threat to citrus posed by this emerging disease is serious and global,



Fig. 1.6 Global distribution of HLB

potentially affecting all regions where citrus is grown. Asia and Africa are the major areas of citrus production, mostly for local consumption (Bove 2006). Brazil and Florida are the major juice producers. South Africa and Mediterranean countries are major exporters (Fig. 1.6).

HLB is probably the most devastating citrus disease known. It is a bacterial disease, unlike most other diseases of citrus. It is caused by the bacterium *Candidatus* Liberibacter asiaticus (CLas). This is a fastidious bacterium, so it cannot be studied in culture. It is quite heat-tolerant and this affects its distribution around the world. Similar diseases of citrus which may or not be classified as HLB, depending on your point of view, are caused by *Ca*. Liberibacter africanus (CLaf)) and *Ca*. Liberibacter americanus (CLam), both heat-sensitive. CLas and CLaf are quite closely related but Clam is distant from them and its emergence)in South America was unexpected.

These are vascular diseases. They are phloem-limited and they infect the whole plant so we need to be aware of what is happening underground alongside the more obvious damage to the canopy. They affect the movement of carbohydrates within the plant, by plugging up the flow of nutrients from the leaves to the roots, or vice versa depending on the season. There are probably other effects on the plant and these are the subject of active research: if we can figure out what the pathogen is doing to the plant, maybe we can stop it. Under the microscope the bacteria are pleomorphic, changing their shape from long flexuous rods to cocci, through an intermediate "lollipop" stage.

Disease Spread

The pathogen is insect-vectored by phloem-feeding specialists, about the size of a flea. The most important species is the Asian citrus psyllid, *Diaphorina citri* (Mann et al. 2018). This is widespread in South Asia and in parts of South and North America. It is not heat-sensitive. The African citrus psyllid *Trioza erytreae* is mainly found in parts of Sub-Saharan Africa. It is heat-sensitive so it tends to migrate into the forests and to higher elevations in the summer months, away from the citrus.

The global distribution of HLB has extended dramatically. First reports of unfamiliar symptoms from China and India were thought to be of a nutrient deficiency. Incidence of what could later be identified as CLas or CLaf spread through South-East Asia into the Middle East and Sub-Saharan Africa. In 2005 Brazil was hit by an unknown condition, first attributed to nutrient deficiency when neither CLas nor CLaf could be found, and then identified as CLam. Since then, CLam is gradually being out-competed and replaced by CLas.

CLas now predominates in Central and North America. The first reported outbreak in Florida was in 2005, preceded by the Asian citrus psyllid as vector in 1998. CLas was then recorded in 2009 in Lousiana, Georgia and South Carolina, in 2012 in California and Texas, and in 2017 in Alabama. The vector has now reached Arizona and Missouri.

Symptoms

Symptoms include appearance of a yellow flag on the tree, twig dieback, blotchy mottle, asymmetrical chlorosis, and misshapen fruits – the top ripening before the bottom (UF/IFAS 2020). New methods of detection using hyperspectral imaging are under investigation (Wang et al. 2019).

Effects on the crop can be drastic (Allen 2017). Orange production in Florida, mainly for juice, has plummeted in the last 5 years. In California the main incidence is on urban trees but the disease is spreading into production areas and similar effects can be expected. The disease affects the root system as well as the canopy. From the psyllid feeding point the bacterium travels rapidly towards the roots. The canopy may remain asymptomatic while 80% of the root system is lost. Control measures must therefore also reach the root system.

Disease Management

Resistance would be the preferred first line of defence. Unfortunately, few sources of resistance or tolerance have been identified in *Citrus*, and breeding a new cultivar by conventional methods may take 20 years. Genetic modification, for example for

an antibiotic trait, may offer an alternative approach. Gene editing, which does not require such exacting regulatory control is an active area of research.

Possible management strategies include:

- Vector control and rogueing of infective trees, requiring numerous applications of insecticide and regular scouting. This works best in large contiguous plantations.
- Fertilizer application, which can improve foliar symptoms but fruit drop and quality are unaffected.
- Thermotherapy: application of sufficient heat to kill the pathogen without severely damaging the host. This can be effective for potted plants but is impractical on a substantial scale.
- Vector exclusion by construction of large insect-proof screens or individual wraps for young trees.
- Antibiotics: but foliar applications do not readily enter the phloem, and trunk injection is time-consuming and costly. Novel compounds are being explored.
- Bactericidal nanoparticles that can enter phloem tissue through foliar application are being investigated.

The Future – Looking Bleak

No single strategy is sufficient for long-term management, which remains problematic. In summary, HLB is an imminent and serious threat to citrus production globally. It is likely to be aggravated by climate change. In Florida, the outlook for the citrus industry looks bleak right now.

Coffee Leaf Rust: A Persistent Threat to the Livelihoods of the People Who Produce Your Morning Cup³

A Devastating Disease

A coffee plantation in Costa Rica in 2012, shown in Fig. 1.7, is representative of plantations in Central America at that time. Most of the plants have lost their leaves and died of infection with coffee leaf rust, caused by the fungus *Hemileia vastatrix* "Hemileia" refers to the half-smooth character of its spores; "vastatrix" means devastating. The pathogen produces spores on the coffee plant that are released and dispersed by wind. They infect other coffee plants, entering through pores and spreading as mycelium in leaf tissue, causing lesions. From these, further spores are released, repeating the cycle – with the potential to cause an epidemic. Coffee leaf rust can cause severe losses to production; for example in Central America in 2012



Fig. 1.7 A coffee plantation in Costa Rica in 2012. Most of the plants have lost their leaves and died of infection with coffee leaf rust

losses were estimated as 20% for the region as a whole, reaching 50% in El Salvador and 75% in certain locations (Avelino et al. 2015).

This is not a new problem. In 1867 there was a severe outbreak of coffee leaf rust in the former British colony of Ceylon (now Sri Lanka). The disease was so damaging that the coffee growers switched to growing tea – and the British became tea drinkers! Coffee leaf rust arrived in the Americas in the 1970s and has been a persistent problem there ever since (Bowden et al. 1971).

Factors Favouring Disease

Outbreaks of coffee leaf rust tend to occur after periods when market prices for coffee are low, because when farm income is low farmers are less able to afford fungicides to control the pathogen, or fertilizers which enable the plant to fight off disease. The market price of coffee has fallen substantially since 2011. Climate is also a controlling factor (Bebber et al. 2016). The pathogen typically thrives at temperatures of 18–23 °C. In 1996 it was unusual to find it above 800 m, but by 2016 climate change had extended its preferred habitats so that the disease could be found up to 1500 m.

Effects on Livelihoods

Thus, we have a fungus, economics and climate change conspiring against the coffee crop, and more importantly conspiring against the people whose livelihoods depend on coffee production (Avelino et al. 2006). For example, the coffee rust outbreak in Central America in 2012–2013 was associated with a demand for labour between 16 and 32% less than in the previous year, with a huge impact on food security (Anonymous 2014). Livelihoods were impacted not only for the 1.5 million unskilled labourers who go from plantation to plantation picking the coffee berries, but also for the 240,000 smallholder farmers who depend on income to feed their families from selling the coffee they produce. In response to this case of food insecurity the World Food Programme supported 53,000 families with 8000 tons of food between July and December 2013, but that was not enough.

The US government responded to the 2012–2013 coffee leaf rust outbreak through the Feed the Future Initiative, launched in 2010 to address global hunger and food insecurity. Alongside research and technical assistance programmes, and financial assistance, we were able to develop a Coffee Rust Global Development Alliance. This is a public-private partnership between the US Agency for International Development (USAID) and World Coffee Research. World Coffee Research is "a non-profit, collaborative research and development program of the global coffee industry to grow, protect and enhance supplies of quality coffee while improving the livelihoods of the families who produce it". It provides a channel for money from the private sector to support research projects, with matching funding from USAID. Projects are led by scientists at Texas A&M University, CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) and other partners.

Options for Disease Management

In the first of these projects the *Coffee Catalog: An interactive website and printed catalog exploring 33 key varieties of Meso-America and the Caribbean* was developed by researchers who went from door to door collecting information about the coffee varieties being grown, their performance, agronomic features, disease resistance and cupping quality (World Coffee Research 2016). Some 20,000 print copies were distributed in Central America, and in 2016 it was accessed online more than 15,000 times. The project also set up regional multi-location trials of varieties from around the world in nine countries. At three locations in each country, 30 varieties were assessed for incidence of coffee leaf rust and other characters. The aim was to identify varieties that might perform better where this damaging disease occurs, especially because many of the varieties grown in Latin America have a high degree of genetic uniformity, rendering them vulnerable to new races of the pathogen, of which many have been identified.

An Arms Race Between Host and Pathogen

Since the epidemic of 2012–2013, coffee leaf rust has been responsible for the loss of 18.2 billion bags of coffee, USD 2.5 billion and 1.7 billion jobs. The crisis is still on. A resistant variety, called Lempira, which has been widely planted since the recent epidemic seems now to have lost its resistance. Plant disease can be represented as an arms race between host and pathogen. In the epidemic of 2012–2013, 13 new races of the pathogen were identified. With huge populations of the fungus and limited variation in resistance of the host there is an inevitable risk of mutations being selected that can be the cause of damaging disease. Researchers are busy working to develop varieties resistant to the current race circulating and to deploy them to plantations so smallholder farmers are able to grow coffee more sustainably.

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