Plant Pathology in the 21st Century

Peter Scott · Richard Strange
Lise Korsten · Maria Lodovica Gullino
*Editors*

# Plant Diseases and Food Security in the 21st Century

Springer

# Plant Pathology in the 21st Century

Volume 10

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Maria Lodovica Gullino, Università degli Studi di Torino, AGROINNOVA, Grugliasco, Torino, Italy

The aim of this Series is to highlight the latest international findings and advances in plant pathology and plant disease management, and plant pathology topic specialist, Congress and Workshop organisers, coordinators of broad International projects are invited to consult with the Series Editor regarding their topic's potential inclusion in the series.

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Cover Illustration: Orange fleshed sweetpotato variety 'Kakamega', showing severe symptoms of SPVD, next to a symptomless plant. Photo: courtesy of Segundo Fuentes.

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# Foreword

Plant pathologists are confronting unprecedented global challenges as we move through the 21st century. These challenges include huge population increases, expanded global trade, unpredictable changes in the climate, and degradation of the lands and water needed for agriculture. In many countries and regions, we face the additional challenges of changing consumer food preferences, which include increasing demands for safe and nutritious foods as well as fresh, local, and organically produced foods. Overall, this means that pathologists cannot focus only on the staple crops for food security. Providing nutritious diets while considering environmental health and stable agricultural systems will require improved, innovative, and broadly applicable approaches and strategies to reduce the overall impacts of plant disease.

An overarching problem for pathologists is that solid, validated data on how the expected future challenges will impact a given disease on a particular crop are available for only a very few interactions. We don't know how environmental stresses (drought, high temperatures, salinity, etc.) will affect the plants and/or the pathogenic or beneficial microbes in the system. That is, we don't yet have accurate information to predict how the phytobiome will respond. For example, for some host/pathogen systems, increasing temperatures lead to more disease, whereas in others, the opposite is true. For some host/pathogen interactions, increasing temperatures render some sources of disease resistance ineffective, resulting in disease, whereas other resistance sources are more effective at high temperatures, and the plants are more resistant to disease. We are just beginning to understand how various microbial components of microbiomes contribute to improved soil and plant health, and which combinations can help to remediate plant disease. While many innovations and technological improvements have been made that will contribute to solving these complex problems, to understand the outcomes for crops critical to a secure and sustainable future, we will need significant collaborative efforts and investments.

The book series Plant Pathology in the 21st Century, coordinated by the International Society for Plant Pathology and the Series Editor Maria Lodovica Gullino, is an important *call to arms* for plant pathologists, identifying the

conceptual, tangible, and technical challenges we face in this century. The series is intended to motivate consideration of the challenges we face in this century. It is entirely appropriate that this edition in the series Plant Diseases and Food Security in the 21st Century be published now, given the proclamation of 2020 as the International Year of Plant Health.

This book in the series reminds us that all of us are impacted by crop diseases, existing or emerging, from our favorite breakfast foods to the staple crops considered essential to food security. Contributing authors use diverse examples to address innovative ways to detect, monitor, and manage plant diseases, and how to model and predict the impacts of diseases on our food system. In recognition of the broader scope of food security, the book contains chapters that address the safety of foods, from pesticide contamination to transmission of human pathogens. All of these factors, including the tools, methods, and innovative strategies, are important, but for successful disease management in the future, we will need robust extension and outreach systems armed with relevant information such that they can transmit actionable guidance to the crop managers and farmers.

As old and new diseases emerge and re-emerge, and changing environmental conditions compound the problems, the global conversations highlighted in this book and others in the series are important steps, but only the first steps. How we, as individuals or as communities of plant pathologists, respond to these needs for action will be important in ensuring food safety and security through the twenty-first century.

President, International Society for Plant Pathology Jan E. Leach
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# Preface

This book is an initiative of the International Society for Plant Pathology (ISPP). It is the 10th in ISPP's book series Plant Pathology in the 21st Century. As part of each of the last five International Congresses of Plant Pathology (1998, 2003, 2008, 2013 and 2018), ISPP's Commission on Global Food Security has coordinated sessions focusing on plant disease as a factor limiting global food security. This book is based on those sessions at the 11th International Congress of Plant Pathology, held in Boston, USA, in 2018, sponsored by ISPP and organized by the American Phytopathological Society.

The editors are grateful for the opportunity to bring together, in this volume, chapters based on a wide variety of presentations at the Congress – bearing on the persistent need for *action* to address the challenges to global food security posed by plant pathogens.

Special thanks are due to Jean Ristaino for coordination of these Congress presentations. We are grateful to the Canadian Phytopathological Society for permission and encouragement to reproduce the Glenn Anderson Lecture as Chap. 3. We also thank the authors of each chapter for their cooperation in making this book.

There are five parts to the book. The first relates to discussions of an expert panel, open to the public. The others relate to four of the formal sessions of the Congress that focused on plant disease and food security.

The book opens with potato blight and the crisis of the 1845 Irish potato famine. E. C. Large's 1940 book *The Advance of the Fungi* opens here too, with a vivid account of Ireland's blighted potato crops and of the continuing struggle to manage the disease. The present book addresses this struggle in the context of food security in the twenty-first century. We have the benefit of greatly enhanced understanding of plant disease mechanisms. Nevertheless, we are inclined to share the realism of Large's 1940 vision of a continuing struggle. The final lines of his book are:

> *Those who believed in genes postulated the existence of an eternal quality, R, which they could take from wild plants, build into the genetical constitution of cultivated ones, and so make them disease-resistant for ever. Those who thought, not in terms of mathematical abstractions, but of the green flux of ever-changing nature, saw little hope of such permanency, and no end to man's labours in defending the crops upon which he depended for life.*

At present, we have a constant reminder of how insidious disease can be, in the form of Covid-19, a viral pathogen of humans, and how failure to acknowledge it promptly turned what could have been a localized epidemic into a pandemic. With plant diseases that affect our crop plants and therefore food security, it is not so much a failure to acknowledge them but the difficulty of identifying their causal agents and finding appropriate techniques to control them. In the first place, there are many species of crop plants that are of importance sociologically and economically, and each has a suite of pathogens. Then, compared with human pathologists, who mainly have to consider only one host organism, humans, there are multiplicities of hosts and pathogens and relatively few plant pathologists to cope with them! However, cope we must if we are to attain the second of the United Nations Sustainable Development Goals – zero hunger by 2030. Already we have over 820 million people who are hungry and over 2 billion who are suffering from hidden hunger – a lack of one or more vitamins or trace elements – and these numbers, far from diminishing, are increasing.

A first task and a fundamental one for controlling plant disease is accurate identification of the causal agent. Not surprisingly, diagnostics feature to varying degrees of prominence in nearly half the chapters in the book. Once the identity of a causal agent of a disease has been established, it is necessary to find a rapid and reliable test, preferably one that can be used in the field, to monitor its occurrence and establish its epidemiology. Speedy action may allow confinement of the disease to a limited area and possibly even its eradication. Second, some assessment of the social and economic costs of the disease should be obtained in order to prioritize the use of usually scarce resources in management and control. Third, if the disease is causing serious social and economic costs, management and control measures must be established to limit these.

Before taking these three points in turn, we would like to draw readers' attention to Chap. 3, which is essentially a biography of Glenn Anderson, a Canadian, who made tremendous contributions to wheat breeding, pathology and the training of young scientists. Norman Borlaug referred to him as his 'green-fingered agricultural scientist' and his General 'Eisenhower' on the frontline in Asia who launched the 'Green Revolution'. He headed the Coordinated International Wheat Program for the Rockefeller Foundation, the Indian Council of Agricultural Research and later, after its creation, the International Maize and Wheat Improvement Center (CIMMYT) in India, 1964–1970. In 1971, he moved to Mexico, becoming Associate Director and, on Norman Borlaug's retirement, Director of CIMMYT. Being a 'doer' he realized that he 'needed boots on the ground' in the wheat-growing areas of less developed countries. As a result, 6-month-long field-orientated training courses for young international staff were initiated in the late 1960s and continued into the 1970s. These were the germ of regional programs in the Andean region and southern cone of South America, North Africa, Middle East, East Africa and West Africa. Sadly, Glenn's life was cut short by leukaemia – but what a legacy he has left in so many parts of the world!

Turning now to diagnostics, a number of novel techniques are described. Chapter 1 starts with an account of potato blight and its profound effects wrought on Ireland

in the 1840s – starvation and mass emigration. Nobody knew at the time what the cause of 'the potato murrain' was, but this was not surprising considering that it predated Pasteur's germ theory of disease. In this chapter, Jean Ristaino and colleagues, using specimens from the original outbreak, amplified three mitochondrial genes and, using Single Nucleotide Polymorphisms (SNPs), were able to show that the 1a mtDNA haplotype was responsible and not the 1b as was originally thought. This work demonstrates the power of molecular techniques in determining lineages of pathogens.

In Chap. 9, Sara Franco Ortega and colleagues call attention to the use of novel serological and molecular diagnostic techniques, exemplified by three important fungal pathogens of rice. They suggest that the LAMP (loop-mediated isothermal AMPlification) assay for on-site detection of pathogens, combined with alkaline extraction of DNA, has great potential for assessing inoculum, including inoculum that is airborne.

Jonathan Shao and colleagues (Chap. 10) describe the use of immune tissue prints and machine learning to detect the causal organism of citrus greening disease, also known as huanglongbing. The organism is an unculturable member of the alpha-proteobacteria '*Ca*. Liberibacter asiaticus'. Cut ends of stems or petioles are pressed onto nitrocellulose paper and a fragment of an outer membrane of the pathogen is detected on the paper by a rabbit polyclonal antibody. A goat anti-rabbit antibody conjugated with alkaline phosphatase and substrate for the enzyme then detects the rabbit antibody. Positives show as dark dots in the phloem. Details of the means by which the tissue prints could be scored using machine learning are given. This allows mass screening of plant material, a necessity for a pathogen that has non-uniform distribution in infected trees.

Three chapters are concerned with the social and economic cost of plant disease. Kreuze et al. (Chap. 5) point out that when sweet potato was introduced from the Americas to Africa over 500 years ago, the varieties were white- or yellow-fleshed, containing no or little beta-carotene, respectively. Beta-carotene is a precursor of vitamin A, which is converted by human metabolism to the vitamin. Sadly but avoidably in sub-Saharan Africa (SSA), 48% of children are estimated to be vitamin A deficient (VAD) – a high social cost as, among other negative effects, VAD is the leading cause of preventable blindness in young children. Efforts are therefore being made to introduce orange-fleshed sweet potato (OFSP), which has high concentrations of beta-carotene, into SSA. Unfortunately, viral diseases have frustrated these attempts. It is a cruel irony that endeavours to counteract the high incidence of VAD in SSA by introducing OFSP are being frustrated by viral infection – more than 30 different viruses are known to infect sweet potato, some in combination completely destroying the crop.

In Chap. 6 Castilla and colleagues review the impact of rice diseases in tropical Asia. They describe a yield- loss model, RICEPEST, originally designed to simulate rice crop growth and development along with injury mechanisms due to pathogens, insects and weeds but sufficiently flexible to be used for other crops. In experiments for Asia overall, mean yield losses owing to diseases, animal pests and weeds were 37.2%.

Epidemic modelling at the landscape level is described with mathematical detail by Fabre and co-authors in Chap. 4. They point out that increased global travel and trade as well as changing climatic patterns have led to the emergence of new and more frequent plant disease epidemics. Mathematical modelling can predict how and where these new arrivals will spread and thus inform and optimize their control. Coding is provided to allow readers to run models for themselves.

In Chap. 7, Petronaitis and colleagues describe the importance of Fusarium diseases of wheat. These are Fusarium headblight and Fusarium crown rot, which are caused by various species of the genus, some of which are also associated with ear, stalk and root rot of maize. The authors provide comprehensive tables showing heavy losses in most wheat-growing areas of the world. Another factor of importance is the production of mycotoxins by these fungi, which killed nearly 100,000 people in Russia in the 1940s (Pitt and Miller 2017). Mycotoxin contamination of food is insidious because dangerous – if not lethal – concentrations may be present in crops such as cereals and legumes – and remain there undetected. One poignant case is the presence of aflatoxin in infant formulations in Ghana. Here, about 40% of deaths of children under 5 years are attributed to malnutrition. In order to counteract this, ready-to-use cereal-legume blends have become available on the market but some contain five times the acceptable limit of 20 ppb aflatoxin. Thus, a policy to improve infant nutrition may have worsened their health (Opoku et al. 2018).

Turning now to disease management, Claire Beverley and Manju Thakur (Chapter 11) point out that 500 million smallholder farmers provide over 80% of the food for a large part of the developing world but they face considerable losses to plant disease. Even if these losses were reduced by as little as 1%, millions more could be fed. They describe a valuable ICT (Information and Communication Technology) tool, which helps farmers to manage pests and diseases of their crops and obtain local news about those that are currently causing concern.

Of course, not allowing pathogens into an area where they are absent is the ultimate disease control method, but with increased travel of people (although currently limited owing to Covid-19) and plants traded widely as commodities, this is becoming increasingly difficult. Mike Jeger and associates (Chap. 8) describe four stages in assessing risks to plant health by the introduction of foreign pests or pathogens: Introduction, Establishment, Spread and Consequences. The European Union's Scientific Panel on Plant Health originally used qualitative methods to assess these four stages but, as explored in the chapter, now provides guidance for their quantitative assessment.

Genetic resistance is the preferred method of control in many instances but it is not always feasible. For example, there are few sources of resistance in *Citrus* to huanglongbing, and breeding a new cultivar by conventional methods may take 20 years (Chap. 1). Genetic modification (GM) could provide a solution but, as is described below, faces stringent regulatory barriers to adoption. In this case, control of the psyllid vector, *Diaphorina citri,* offers an opportunity but involves numerous applications of insecticide, regular scouting and rogueing of infective trees.

Ploetz (Chap. 2) points out that there are convincing arguments for using GM (although it is a technique banned by several countries of the European Union) to

produce genotypes of premium bananas such as Cavendish with resistance to Fusarium wilt. For example, Grand Nain, a Cavendish cultivar, transformed with a nematode-derived gene, Ced9, remained resistant even to the much-feared TR4 strain of the causal organism during a 3-year trial. However, a line transformed with the RGA2 gene from another *Musa* species, *Musa acuminata* ssp. *malaccensis,* also showed resistance in the trial. Homologs of the RGA2 gene are present in wildtype Grand Nain but were expressed at levels 10-fold lower than in the most resistant transgenic lines. Dale et al. (2017) suggested that the expression of RGA2 homologs 'might "be elevated through gene editing, to provide non-transgenic resistance", which would therefore avoid anti-GM scrutiny'. No doubt the authors were disappointed to learn that, in 2018, the European Court of Justice characterized gene editing as a form of GM, showing that the Court is incapable of distinguishing a technique from its product. Of course, any new variety of crop plant should be tested rigorously for unwelcome properties, but to deny millions of the world's still increasing population the benefits of important crop varieties simply because of the way they are produced seems crass.

The last two chapters of the book are concerned with food safety. Nicola Holden (Chap. 13) draws attention to the fact that edible plants can be important vehicles for the transmission of human pathogens and that there are molecular parallels between human pathogens and plant pathogens in the triggering of defence responses in their hosts. She suggests that such parallels could be exploited in shared dialogue and research.

Carmen Tiu (Chap. 12) points out the necessary role that pesticides play in integrated pest management of our crops, and therefore in food security, but emphasizes the importance of limiting the unwanted traces they may leave in food. Unacceptable levels of pesticide residues are defined by Maximum Residue Limits (MRLs). The effectiveness of MRLs depends on widespread acceptance, for which simpler protocols are urgently needed: an outline scheme is proposed.

Readers of this book will find it contains much food for thought, which – it is hoped – will be transformed into food for people and achievement of SDG2 – zero hunger by 2030. For this, to use Glenn Anderson's phrase, 'boots on the ground' will be needed.

Oxford, UK — Peter R. Scott

London, UK — Richard Strange

Pretoria, Republic of South Africa — Lise Korsten

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# Part I
# Crop Diseases Threaten Global Food Security and Your Breakfast

# Chapter 1
# Potatoes, Citrus and Coffee Under Threat

**Jean Beagle Ristaino**

**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 blight**[1]
  A disease with a historical link to famine and ongoing potential to threaten a staple crop
- **Huanglongbing of citrus - Megan M. Dewdney**[2]
  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.

[1] The 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.*

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

[3] Based 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 Ile in Quebec resulted in the spread of human diseases and thousands more perished *en route*. At a mass burial site in Grosse Ile, 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

**Fig. 1.5** Herbarium specimen of potato infected with *Phytophthora infestans* collected by J Errikson, Stockholm, Sweden in 1882

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 mid-twentieth 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 climate-adapted 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 Table[2]

### *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,

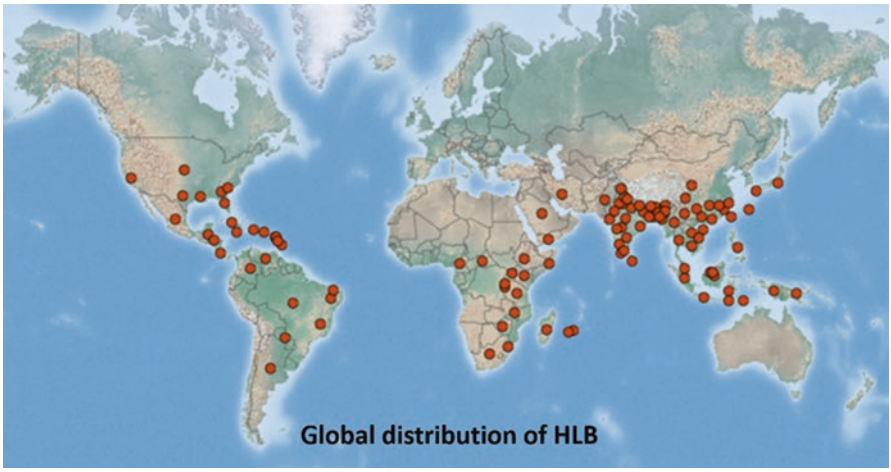


**Fig. 1.6** Global distribution of HLB

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 Cup[3]

### *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).