Pathogens and Quarantines

CHAPTER 3

When the potato, Solanum tuberosum, was transported from its native home in South America to Europe, a new and important food crop began its journey to all parts of the world. Today the potato is the fourth most important world crop—behind rice, wheat, and maize (corn)—and the rate of increase in its production is greater than that of any other crop. It is grown in climates similar to those of the cool South American highlands, but some cultivars are adapted to warmer climates, thus extending its range to tropical lowlands as well. It is grown in each state in the United States and in hundreds of countries on many continents. About 200 years after its introduction to Europe, one of the important fungal parasites of the potato inadvertently crossed the ocean in infected tubers, leading to late blight epidemics and human starvation. Since no one understood the nature of plant disease at that time, there could be no safeguards to prevent such an introduction. Phytophthora infestans is now an established pathogen in all potato-growing areas of the world, along with various other fungi, bacteria, viruses, nematodes, and other pathogens that traveled along with the tubers of their host.

How to move useful and important plants around the world without transferring dangerous pathogens and pests is one of the great difficulties facing the human race. We now know that foreign pests and parasites represent a dangerous threat to native plants. If a pest is capable of attacking a plant, the initial exposure can be disastrous because the plant is not likely to have defenses against the attack. After years of selective pressure, plants evolve various means of resistance to their attackers, but at the first exposure, they have not had the opportunity to coevolve with the pest to create a genetic balance. Without well-developed resistance mechanisms, plant losses can be great.

Also vulnerable are the various introduced species that have been removed from the selective pressure of pests or parasites in their native land. This occurred with the potato in Europe and many other species that have been moved to new continents. During this “protected time,” the plants usually become quite uniform genetically to meet the agricultural requirements of farmers, and, in the absence of the pest or parasite, they have no means of selectively maintaining resistance. When a pest or parasite is then accidentally introduced to the new land, the threat of disaster is great because of reduced resistance and reduced genetic diversity.

As human travel increased and the time required to cover long distances decreased, plants and, unfortunately, many of their parasites were collected and distributed to new lands. The primary production of certain crops
has shifted to areas far from their place of origin to escape native parasites. With the birth of the science of plant pathology in the 1840s, people began to understand the role of introduced pathogens in some of the important epidemics of that time. They also began to see how some traditional agricultural practices make crops more vulnerable to plant diseases. But many of these lessons were accompanied by tremendous economic loss and important changes in the agricultural development of the areas in which these epidemics occurred. Major changes in agriculture always have political and economic consequences. This chapter describes some historical examples of pathogen movement and agricultural practices that led to epidemics and how quarantine legislation helps protect plants within political borders against invasion by dangerous pests and parasites.

Coffee Rust

Coffee is a crop of the tropics surpassed only by oil in its value as a world commodity. For centuries, it has been a significant import crop in Europe and economically important to the European countries that ruled tropical colonies. It remains an important crop to the independent nations created from those colonies.

Coffee became a popular drink in Europe in the 1600s when contaminated drinking water limited people to fermented beverages or those made with boiled water, such as tea or coffee. Coffee houses were major social centers in England in the 1650s. The Dutch were the first major European coffee importers, transporting coffee from their colonial plantations in Ceylon (now Sri Lanka), Java, and Sumatra. The small, nondeciduous tree, * Coffea arabica, produces red berries that contain the seeds or beans that are roasted and then brewed into a potent caffeinated drink. The trees grow best in cool, humid climates but cannot survive frost and are thus limited to tropical highlands.

During Napoleon's time, much of the coffee-producing area was lost to the Dutch by the English. In 1825, the British began development of their property in Ceylon (now Sri Lanka), and every suitable piece of land was planted to coffee plantations. By 1870, Ceylon was the world's greatest producer of coffee. Java remains a slang term for coffee, reflecting the time when coffee production centered in that part of the world. Today, however, 90% of the world's coffee comes from the tropical Western Hemisphere. Sri Lanka is now known best for its tea production, and the cup of tea, rather than coffee, has become a familiar part of England's culture. As with the Irish potato famine, a fungus was responsible for these changes, but only because of the agricultural practices of human beings.

The fungal parasite probably arose in southern Ethiopia, the origin of the coffee plant itself. It is a Basidiomycete, a fungal group containing many important plant parasites, and belongs to a subgroup known as the rusts. The rusts are such important plant pathogens that they are discussed in detail in Chapter 10, and the complete biology of the coffee rust fungus is explained there. It is sufficient at this point to consider the problem of a rapidly reproducing fungus capable of infecting the foliage of the coffee tree, a nondeciduous, perennial plant that grows in a frost-free climate.

A single tiny rust pustule on a coffee tree leaf can produce 150,000 spores, and a single leaf can contain hundreds of pustules. When the coffee rust fungus, * Hemileia vastatrix, reached Ceylon in 1875, nearly 400,000 acres (160,000 hectares) were covered with coffee trees. No effective chemical fungicides were available to protect the foliage, so the fungus was able to colonize the leaves until nearly all the trees were defoliated. The spores produced on the leaves are quite resistant to desiccation, unlike the sporangia of * P. infestans, and are capable of long-distance movement in a viable

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**Fig. 3-1.** Coffee (*Coffea arabica*) with the berries that contain the seeds or "beans" that are harvested and roasted.

**Fig. 3-2.** World distribution of the coffee rust fungus, with the dates it was first discovered.
state. They easily moved through the acres of coffee trees, feasting on the banquet prepared by unsuspecting plantation owners. In 1870, Ceylon was exporting 100 million pounds (45 million kilograms) of coffee a year. By 1889, production was down to 5 million pounds (2.3 million kilograms). In less than 20 years, many coffee plantations were destroyed, and production had essentially ceased.

![Symptoms of coffee rust infection](image)

**Fig. 3-3.** Symptoms of coffee rust infection (*Hemileia vastatrix*).

**H. Marshall Ward,** a student of Anton deBary, was sent to Ceylon by the British government to save the coffee plantations. Even though he failed, he presented the infant science of plant pathology with two important concepts that are still fundamental to plant protection. His studies of the life cycle of the rust fungus convinced him that the germinating spores represented a vulnerable stage for attack. He recommended that, to effectively protect the plant from invasion, fungicides should be present as a protective coating on the leaves before the spores arrived. Once infection had occurred, the hyphae inside the leaf tissue were no longer vulnerable to the fungicide. Thus, it was important to anticipate the disease and not to wait for symptoms to appear before spraying was initiated. Unfortunately, the sulfur fungicides of that time were neither readily available nor very effective, and the rust epidemic was too well established to save the coffee trees.

Ward also warned about the dangers of monoculture. He observed that the continuous plantings of coffee trees over the island had created a perfect environment for a fungus epidemic. Rusts, like downy mildews, are obligate parasites and require living host tissue for their growth and reproduction. The rapid epidemic of the coffee rust was enhanced by the many acres
of the host plant. His warnings, unfortunately, were ignored, and most of the dead coffee trees were replaced with tea bushes. Luckily, no fungus immediately invaded the tea crop, and newly discovered fungicides were soon available to protect the tea from its fungal parasites.

In an attempt to escape the rust disease, coffee production moved to the Western Hemisphere. Coffee had been grown in the Caribbean Islands since the 1700s, but plantings quickly spread to the tropical highlands of Brazil, Colombia, and Central America. Today, Brazil, followed by Colombia, dominates the world coffee market. Coffee production centers in the tropical Americas because the coffee rust was successfully excluded by careful quarantines.

The quarantine was successful for over 100 years, but, in 1970, coffee rust was discovered in Brazil. It is not completely clear how the fungus arrived in Brazil, but intercontinental movement of the rust spores from coffee plantations in East Africa is a likely means. The dust-like spores could also have been easily carried on luggage, people, plants, or airplanes that continuously move between the continents. Eradication of infected trees has failed to eliminate the parasite, and the fungus has slowly spread throughout the coffee-growing areas, moving into Colombia and the countries of Central America. The spread was delayed by careful quarantines between many of the countries, but political unrest and human travel, along with natural dispersal of spores by wind, have allowed the fungus to circumvent the quarantines.

What will be the consequences of the importation of such a dangerous pathogen? Frequent fungicide applications will be necessary to protect the highly susceptible cultivars of C. arabica, which produce the best quality of coffee. Chemical inputs are particularly demanding for small growers, who now must purchase fungicides and spraying equipment. Trees must be grown at lower densities to allow complete fungicide coverage of the susceptible foliage. Wider spacing of trees also increases air movement between the trees. When the foliage dries more quickly, infections are reduced since, like almost all fungal spores, rust spores require water for germination. Chemical inputs and changes in planting practices increase the costs of production and hence the price to consumers.

Rust-resistant cultivars of C. arabica and other species such as C. canephora exist, but the crop is of poorer quality. Plant breeders must often struggle with the problem of combining desirable genetic traits for crop quality with genes for resistance in the same plant. Rust fungi are capable of producing many genetically different races, and 32 races of H. vastatrix have been detected. It is always particularly difficult to find durable resistance to a pathogen when the crop is a perennial growing in a frost-free environment. The pathogen population is not reduced by winter stresses, and replanting with new cultivars is expensive and infrequent. Resistance that is effective against all races of the parasite remains the long-term goal. In the meantime, fungicide applications are becoming part of the routine production practices on coffee plantations in the Western Hemisphere.

South American Leaf Blight of Rubber

While the British switched to tea production as a result of the coffee rust epidemic, many of the remaining Dutch holdings in southeast Asia became important rubber plantations. Like the potato, the rubber plant had its origins in South America. Until the year 1900, almost all rubber production was in Brazil and Peru. Once again, a fungal parasite is at the center of our story, greatly assisted by the agricultural practices of human beings.

The rubber plant, Hevea brasiliensis, produces natural rubber in a latex sap contained in a system of tubes throughout its trunk. Over 12,000 species of plants exude a milky latex, including such familiar species as milkweed,
poppy, lettuce, poinsettia, and their relatives. The exact function of the latex is not known, but, in some cases, it contains compounds that protect against insect pests. The latex of many of these plants contains the polymer compounds known as rubber, and the latex of *H. brasiliensis* is a particularly efficient source, containing 40–50% rubber. In the days before the abundant variety of plastics and other polymers derived from oil, there were many industrial, medical, and household needs for a durable and flexible waterproof substance. In 1840, Charles Goodyear developed the process of vulcanization that made rubber tough and resistant to melting at high temperatures but not brittle in cold weather.

With the advent of motorized vehicles, the demand for rubber greatly increased for use in tires. Unfortunately, rubber trees grew in the jungles of South America at very low densities, only a few in a single acre. Rubber was collected by natives who cut down whole trees and collected the mass of latex that bled from the tree. This process became very inefficient as the collectors were forced to travel farther and farther into the jungle searching for rubber trees.

Seeds of these valuable plants were smuggled out of South America by an Englishman, H. A. Wickham, in the 1870s. Plantation production was begun in Asia after a tapping system was developed that allowed the latex to be repeatedly harvested from the trees without killing them. Plantation production followed in South America as jungle harvesting became more and more difficult. Following World War I, there was particular pressure to develop plantation rubber in South America to provide secure sources of rubber for the United States in times of war. Henry Ford developed 8,000 acres (3,200 hectares) in Brazil for rubber production in 1929, but once again a microscopic fungus was responsible for the failure. The trees were all killed by a disease called the South American leaf blight, resulting from infection by the fungus *Microcyclylus ulei*.

This fungus is a member of the Ascomycetes, a major fungal group mentioned in Chapter 2. The mycelium of an Ascomycete can be easily distinguished from that of an Oomycete due to the presence of septa, or crosswalls, that separate a hypha into compartments. Such hyphae are described as septate to separate them from the nonseptate hyphae of Oomycetes. In Ascomycetes, the number of haploid nuclei in each compartment can vary because each septum contains a pore that allows nuclei and cytoplasm to move throughout the mycelium.

As with many other fungi, both sexual and asexual spores are produced. The asexual spores, known as conidia, are important in the rapid reproduction of the fungus but represent no genetic variation except that produced by mutation. Conidia of *M. ulei* are produced on the surface of infected leaf tissue, where they are easily dispersed by air to other plants. Only a few days after infection, conidia begin to be produced in numbers too large to imagine, continually infecting the tender new tissue of young leaves.

*M. ulei* also produces a survival stage through sexual reproduction (Fig. 3-8). The vegetative mycelium is haploid, and, at the time of sexual reproduction, a nucleus from a male structure (often an antheridium) joins the nucleus in the ascogonium (analogous to the oogonium of the Oomycetes). The nuclei divide in tandem to produce a limited dikaryotic mycelium. In the ascus mother cells, karyogamy results in a series of diploid nuclei, each of which immediately undergoes meiosis to produce four haploid nuclei. These nuclei undergo mitosis to produce eight nuclei, each of which becomes enclosed by a wall and some cytoplasm to form an ascospore. Each set of ascospores is produced in a sac, or ascus, which is characteristic of sexual reproduction of all members of the Ascomycetes. Asci (the plural of ascus) often contain four or eight ascospores because they are the products of meiosis (four ascospores) and frequently a secondary mitosis (eight ascospores).

The asci are produced in a vaselike perithecium, a protective fruiting body that usually consists of dark-colored hyphae that are resistant to desiccation. In addition to their ability to survive adverse conditions, ascospores also represent a genetically diverse new generation because they are a product of meiosis and genetic recombination. The ascospores are forcibly discharged through an opening at the top of the perithecium by a puffing mechanism caused by changes in humidity as drier air passes by the liquid-filled asci. This small propulsion is sufficient to send ascospores on a journey to other rubber plantations or to renew an epidemic in the home plantation.

The Ascomycete group includes many important plant pathogens and other well-known fungi as well. Probably the best known Ascomycetes are the yeasts, so important in the production of bread and alcoholic beverages. Rather than having the mycelium of typical fungi, the yeasts have a vegetative structure that is reduced to single cells that bud to produce new cells (Fig. 3-9). Sexual reproduction involves the fusion of the nuclei of two single cells, followed by meiosis, resulting in an ascus of ascospores.

![Fig. 3-8. Diagram of generalized ascus formation. A, Male structure (often an antheridium) and female structure (ascogonium); B, the male structure contributes nuclei to the female structure; C, a limited dikaryotic mycelium develops in which each cell contains two genetically different nuclei; D-F, through a complex mechanism, a single cell, the ascus mother cell, becomes delimited; G, karyogamy occurs and the two nuclei fuse to form a single diploid cell; H, meiosis produces four haploid nuclei; I, in many Ascomycetes, mitosis follows meiosis to produce eight haploid nuclei, and the sac, or ascus, containing the nuclei elongates; J, a spore wall forms around each nucleus. The ascus now contains eight ascospores.](image-url)
Brightly colored, cup-shaped saprophytic fungi on decaying wood and the morel mushrooms of gastronomic fame are the reproductive structures of other familiar Ascomycetes. Microscopic examination of their surfaces reveals masses of asci containing ascospores.

We should now consider why *M. ulei* destroyed the South American plantations but did not destroy the rubber trees in the jungles. The answer lies solely in the density of planting. All plants are parasitized by relatively harmless leaf spot fungi. If a rubber plant in the jungle becomes infected by *M. ulei* and spores are produced, the probability of those spores landing on another rubber plant is very small. The low density of the rubber trees, combined with the dense foliage of surrounding plants, protects rubber plants from frequent infections. In plantations, however, there is no blocking foliage of nonhost plants, and plants exist in high densities, creating the perfect environment for an epidemic, especially in the continuous warmth and moisture of the tropical climate. It is not surprising that this previously minor parasite became a deadly pathogen in plantations.

The plantations of Southeast Asia were, and are, just as vulnerable to
destruction, but they have been able to exist on a continent without the leaf blight fungus, the mirror image of coffee production. Rubber plantation workers are trained to recognize the lesions of *M. ulei*, and continual vigilance has kept the Asian plantations blight-free so far. Back in Brazil, only repeated fungicide applications ensure protection against the continuous supply of spores in a plantation environment. Genetic resistance has been investigated, but trees resistant to the fungus yield less rubber than the more susceptible ones. Disease-resistant tops can be grafted onto high-yielding root stocks, but the process is costly. Brazil, the site of origin of the rubber tree, is now an importer of natural rubber. Asian plantations, created from the fungus-free seeds smuggled out of South America, produce 90% of the world’s natural rubber. Only a strict quarantine and many miles of ocean have prevented devastation of the Asian plantations.

**The Need for Quarantines**

Both coffee rust and South American leaf blight of rubber are examples of how monoculture agriculture increases the danger of major epidemics. In today’s agriculture, most crops are placed in similarly precarious situations. A field or orchard planted with hundreds or thousands of plants of a single species is a generous invitation to any parasite. In perennial and tropical environments, the danger is even greater because susceptible plant tissue may be continually available, and winter stresses do not reduce the parasite population. For both rubber and coffee production, escape to another continent was the most effective solution. Rubber remains safe from leaf blight in Asia, but coffee producers must now learn to coexist with the rust fungus throughout the world.

Three important plant disease epidemics that occurred in the early part of the 20th century led to the first U.S. quarantine legislation in 1912. In two of the epidemics, native plants were killed by introduced parasites to which they had little resistance. The chestnut tree, *Castanea dentata*, a dominant species throughout the Appalachian mountain range, was nearly eliminated by a fungus from Asia, and the eastern white pine, *Pinus strobus*, suffered tremendous losses to a fungus introduced from Europe. Citrus is an introduced crop in America, but a serious bacterial disease, citrus canker, was also introduced to the citrus orchards at about the same time. All three diseases have important histories and will be discussed in greater detail in later chapters.

Following these epidemics, it became clear that open borders and unrestricted import of plants and plant products such as fruit, nuts, and lumber threaten important native and agricultural plants. It was also clear that the continued import of plants and plant products was necessary for agriculture and the economy. The world map showing the origin of many food crops (Fig. 3-12) makes it obvious that our agricultural production would be excessively limited if it were restricted to plants native to North America.

Microscopic parasites in plant tissue are very difficult to detect, unless the infection is well established so that lesions of dead cells or other symptoms