

## CHAPTER 4

# *Invasions of Natural Ecosystems by Plant Pathogens*

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### 4.1 INTRODUCTION

Disease epidemics have had a great influence on the history of mankind. While most disease epidemics have involved humans, crops and domesticated animals, natural ecosystems have not gone unscathed. Invading plant pathogens have led to some of the most serious disruptions of natural ecosystems ever recorded. The devastating impact of chestnut blight on North American hardwood forests and of *Phytophthora* root rot on Western Australian jarrah forests are two striking examples.

This paper examines the extent, modes and patterns of invasions of natural ecosystems by plant pathogens not originating in these ecosystems. Agricultural systems, cultivated forests and forests whose natural vegetation structure has been significantly altered are excluded from the concept of natural ecosystems used here. Pathogens occurring on invasive plants in natural ecosystems are not considered invasive unless they cause epidemics in the indigenous vegetation.

In this chapter I address a number of important questions about invasions of natural ecosystems by plant pathogens on a global basis. How successful have plant pathogens been in invading natural ecosystems? Are there any similarities amongst modes of invasion by plant pathogens? What has been the human role in successful invasions? What can we expect in the future? Are there promising management strategies that can be employed?

### 4.2 SUCCESSFUL INVASIONS

The extent and effects of invasions of natural ecosystems by plant pathogens can probably best be appraised by examining some successful invasions. The following descriptions of successful invasions also provide the basis for further analysis of the underlying patterns common to such invasions.

#### 4.2.1 Chestnut blight

The destruction of the American chestnut, *Castanea dentata*, is one of the best known and most devastating results of an invasion by a plant pathogen.

*Cryphonectria parasitica*, the chestnut blight fungus, was introduced into North America on ornamental nursery material from Asia late in the 1890s (Walker, 1957). Quimby (1982) and Horsfall and Cowling (1978) provide much information regarding the impact of the disease. From the original introduction in New York, the pathogen spread throughout 91 million hectares of hardwood forests of the eastern USA in less than 50 years. The chestnut was the dominant tree in large areas of forest and composed up to 25% of some forests. Chestnut blight virtually eliminated the American chestnut throughout its natural range. In the words of Harper (1977), 'This is probably the largest single change in any natural plant population that has ever been recorded by man.'

#### 4.2.2 White pine blister rust

The white pine blister rust fungus, *Cronartium ribicola*, is indigenous to Asia and southern parts of Europe (Bingham *et al.*, 1971). The fungus was introduced from Europe into the New England area of North America in the early 1900s on white pine nursery stock. It is also thought to have been introduced into British Columbia, Canada, at about the same time. Blister rust rapidly became epidemic in northern populations of highly susceptible five needle pines (Walker, 1957). The disease is especially severe on seedlings and young trees. Although the rust requires *Ribes* spp. as an alternate host to complete its life cycle, susceptible currants and gooseberries occur along with five needle pines throughout their natural ranges in both North America and Eurasia. Extensive *Ribes* eradication programs were carried out to try to control the disease, especially in managed forests, but these were not effective.

#### 4.2.3 Dutch elm disease

Dutch elm disease, which first appeared in Europe in the early 1900s, received its name because of its rapid spread through elm populations in Holland. Shortly after that, the fungus causing the disease, *Ophiostoma ulmi*, was introduced to North America on diseased timber from Europe. The pathogen's natural vector, the European elm bark beetle, was also introduced to North America at about the same time (Bingham *et al.*, 1971). The disease spread rapidly throughout American elm populations, aided by both its introduced vector and an American elm bark beetle, (Quimby, 1982). Elms from eastern Asia are resistant and this area is believed to be the origin of the fungus (Bingham *et al.*, 1971; Horsfall and Cowling, 1978). An interesting aspect of this disease is that recent outbreaks of the disease in Europe apparently have resulted from the introduction of more pathogenic strains from North America (Brasier, 1979). Logs used as dunnage in ships have been implicated in these recent introductions.

#### 4.2.4 Pine wilt disease

The pine wood nematode, *Bursaphelenchus xylophilus*, was introduced into Japan in the early 1900s on diseased timber. Mamiya (1983) has recently reviewed the development of the epidemic caused by this insect-vectored nematode. The nematode was spread amongst the Japanese islands by the movement of infested timber and locally disseminated by a native insect vector, the Japanese pine sawyer. Pine wilt disease has affected more than 650 000 hectares or 25% of Japan's 2.6 million hectares of pine forest and killed more than 10 million Japanese pine trees. The pine wood nematode was not recognized as the cause of the epidemic until the early 1970s. Subsequently, the nematode was found in North America, where it is considered to be indigenous (Wingfield *et al.*, 1984).

#### 4.2.5 *Phytophthora* root disease

The most dramatic and well-known invasion of a natural ecosystem by a plant pathogen in the southern hemisphere, is the invasion of the jarrah forests of Western Australia by *Phytophthora cinnamomi*. However, this root fungus has also invaded other natural ecosystems. *Phytophthora cinnamomi* has a host range of nearly 1000 different plants, including many in natural ecosystems (Zentmyer, 1980). This pathogen is therefore different from the other pathogenic invaders considered above.

The background and salient features of the jarrah forest invasion are covered in recent reviews (Shea, 1976; Zentmyer, 1980). *Phytophthora cinnamomi* is presumed to have been introduced to Western Australia on diseased nursery material from eastern Australia. More than 300 000 hectares of jarrah forest have been affected by this disease. Water supplies of the region are threatened by increasing salination due to loss of forest cover. Spread of disease within the forests was facilitated by roadbuilding, logging and mining activities that involved movement of soil or gravel containing the fungus. From roadsides and other points of introduction, the disease moved into forests along drainage lines. The canopy vegetation of the forests is comprised almost entirely of the highly susceptible jarrah (*Eucalyptus marginata*). The situation was further aggravated by altered fire regimes that favored more susceptible understory vegetation. Widescale quarantine has been implemented to protect areas not yet affected by the disease.

Eucalypt forests in Victoria, Australia have also been invaded by *Phytophthora cinnamomi* (Weste and Taylor, 1971). The effects on the canopy vegetation have not been as great as in Western Australia, but a greater number of plant species have been affected. More than half the species in plant communities have been destroyed in some places. The pathogen was presumably introduced to that region on diseased nursery material.

The earliest known invasion of a natural ecosystem by *Phytophthora cinnamomi* occurred sometime in the 19th century in the forests of the southeastern USA (Crandall *et al.*, 1945). Chestnut root disease spread rapidly throughout these forests and eliminated the chestnut in its southern range long before chestnut blight appeared in the northeastern USA. Certain native *Pinus* spp. were also affected and the disease on pines became known as little leaf disease. The means of introduction of the pathogen is not known.

*Phytophthora cinnamomi* has been involved in tree mortality in other forest ecosystems including the *Nothofagus* forests of Papua New Guinea (Arentz, 1983), the rain forests of northeastern Australia (Brown, 1976), the ohia forests of Hawaii (Kliejunas and Ko, 1976), and the afro-montane forests of South Africa (Von Broembsen *et al.*, 1986). However, it is not clear in these cases whether the fungus is an introduced invader or a native pathogen.

The center of origin of *Phytophthora cinnamomi* is believed to be the Australasian region (Zentmyer, 1980). However, recent evidence (Von Broembsen and Kruger, 1984) indicates the fungus is also indigenous to South Africa. This suggests that the fungus may once have had a wide southern distribution before the breakup of Gondwanaland and that the present disjunct natural distribution has arisen through vicariance. Superimposed on this natural distribution is dispersal by movement of the fungus on cultivated plants. The origin of the *Phytophthora cinnamomi* occurring in a particular natural ecosystem thus can be difficult to determine.

### 4.3 PATTERNS AND MODES OF INVASION

From the information available on successful invasions, a number of patterns are apparent. The most obvious is that there have been relatively few successful invasions of natural ecosystems by plant pathogens. Micro-organisms are relatively inconspicuous and undoubtedly some invasions have not been recognized. However, plant disease epidemics seldom occur in undisturbed natural ecosystems (Harlan, 1976). Moreover, except for certain unspecialized pathogens, most pathogens are able to attack only a very limited number of closely related host species, and the possibility of finding a susceptible host in a new ecosystem is low.

#### 4.3.1 The invaders

The successful invaders represent three of the five kingdoms of living organisms (Margulis and Schwartz, 1982) and include nematodes and both lower and higher fungi. Bacterial and viral phytopathogens are conspicuous by their apparent absence. One of the successful invaders, *Phytophthora cinnamomi*, is a generalist pathogen and has invaded several different natural ecosystems at the expense of a wide range of plant species. Host specificity is not an important constraint for a

generalist invader, thus there are potentially more ecosystems that could be invaded by generalist pathogens. The remaining invaders are specialist pathogens that cause epidemics only on groups of closely related species. None of the specialist invaders are important pathogens at their centers of origin.

Complex life cycles do not seem to deter invasion of natural ecosystems by plant pathogens as has been suggested for invasions by animal and human pathogens (Dobson and May, 1986). Several of these successful plant pathogenic invaders depend on insect vectors or alternate hosts to complete their life cycles. In at least one case (Dutch elm disease), an insect vector was also introduced. Local insect vectors proved suitable for other invaders.

#### **4.3.2 The invaded ecosystems**

All of the successfully invaded ecosystems are temperate forests with climates similar to the areas of pathogen origin. All of the devastating invasions were facilitated by the marked susceptibility of fairly uniformly distributed, dominant trees of one or a few closely related species. Harlan (1976) has suggested that forests of the wet tropics are not good candidates for epidemics because of their heterogeneity. However, other important regions such as the taiga, tropical savanna, grassland steppes, and desert shrublands are often characterized by vast uniform stands of one of a few dominant species. It is not clear whether these regions are climatically unsuitable for successful invasions by plant pathogens or merely awaiting the arrival of invasive pathogens.

An obvious but significant characteristic of the successfully invaded ecosystems is that they have been separated from the ecosystems where the invasive pathogens originated for a considerable period of time by geographical barriers. The resulting isolation means that more susceptible genotypes that might have been eliminated or suppressed in the presence of the pathogen would not be constrained by this factor. Hosts that have evolved in the absence of their previous pathogens are often more susceptible than their constantly challenged relatives. When the physical barriers between the isolated regions are bridged, the consequences can be disastrous.

#### **4.3.3 The human role**

One of the most important patterns evident is that all of the pathogens that have successfully invaded natural ecosystems have been introduced to these regions by humans. Inter-continental dispersal of viable propagules of plant pathogens by air streams certainly occurs, and is believed to have been responsible for the movement of a few agricultural pathogens across immense ocean barriers (Harlan, 1976). However, humans have been a much more efficient agent of dispersal. Throughout history, cultivated plants and their pathogens have been carried to new regions of human colonization and development. Thus, humans

have been responsible for moving many plant pathogens, of which only a few have invaded natural ecosystems. All of the successful invaders discussed above were introduced on diseased nursery material or timber prior to strict implementation of quarantine.

Fox and Fox (1986) have suggested that disturbance is a prerequisite for invasion of natural ecosystems by plants and animals. In the case of *Phytophthora* root disease, invasions have apparently been facilitated by disturbance of natural ecosystems. However, disturbance does not seem to be essential for invasions of natural ecosystems by plant pathogens.

#### 4.4 CONCLUSIONS

It is important to consider whether management strategies, which will act to constrain future invasions, can be implemented. From the preceding analysis, certain strategies would seem to be indicated. The mode of spread of invasive plant pathogens is similar. All the invaders were human introductions before the institution of effective quarantine policies. The introductions have occurred on diseased nursery material or timber. The pathogens were thus introduced with suitable host material that served as temporary repositories from which subsequent invasions took place. The possibility that inoculum from this material could establish on susceptible hosts would be greater than for inoculum not associated with host material.

Quarantine has apparently been effective in limiting invasions. Quarantine efforts should, therefore, be emphasized and given greater support. The movement of high risk materials such as rooted nursery stock and barked timber between and within countries is now generally prohibited. Some problems regarding ornamental nursery stock, timber, dunnage, and packing materials are still evident. Where movement of such materials is not prohibited, this ought to be implemented. Quarantine programs in Third World countries, where facilities may not be adequate to exclude potential invaders, require additional support.

The paucity of successful invasions of natural ecosystems by plant pathogens pays tribute to the powerful natural mechanisms operating to prevent such invasions. The operation of these mechanisms in natural ecosystems needs to be fully investigated and more clearly understood. A general management policy that minimizes the alteration of intact ecosystems so that these protecting mechanisms can remain fully operational seems prudent. This is especially important for temperate forest ecosystems, which are apparently more susceptible to invasion. This protectionist policy would also minimize epidemics that are caused by indigenous pathogens and that frequently result from disturbances.

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