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Phytophthora Pathogens of Trees: Their Rising Profile in Europe

INFORMATION NOTE

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SUMMARY

Phytophthoras are a group of microscopic fungal pathogens responsible for major plant diseases in many parts of the world. A number of Phytophthoras are tree root pathogens, but they have made little impact in European woodlands until recently. During the 1990s their profile has increased in Europe due to the demonstration that *Phytophthora cinnamomi* is associated with mortality of evergreen oaks in Iberia, that an unusual new *Phytophthora* is responsible for the death of riparian alders across Europe, and that certain Phytophthoras may be involved in the dieback and decline of pedunculate oak. This Note outlines the biology and ecology of the pathogen, the background to the renewed interest in Phytophthora root diseases of trees, and research in progress to evaluate their significance to UK forests.

INTRODUCTION

1. *Phytophthora* (from the Greek for 'plant destroyer') is a genus of some 60 species of plant pathogens. Some are responsible for major epidemics, such as the potato blight pathogen, *P. infestans*; or for destabilising entire natural ecosystems, such as the Western Australian 'jarrah dieback' fungus *P. cinnamomi*. Phytophthoras produce microscopic swimming spores (zoospores) that infect the host during wet periods. Free water is therefore usually required for infection, though not for subsequent development of the pathogen in host tissue. In trees it is principally the fine roots or the collar region that are attacked initially. The fungus may then spread to larger roots or up into the trunk, the infected tissue being mainly the inner bark (cambium and phloem).

2. Long distance spread of the pathogen is often via infested soil or plant material. Indeed, there has been enormous and increasing international spread of *Phytophthora* pathogens, by man, during the past 200 years, and many of the more serious diseases caused by Phytophthoras probably result from introduction of the pathogen to a new and susceptible host. Locally, where conditions favour rapid build-up of zoospore levels and trees are genetically or seasonally susceptible, episodes of acute disease can occur, trees dying suddenly from water stress due to loss of fine roots or due to stem girdling. Under other conditions, zoospore populations may remain low, resulting in chronic disease levels, with root loss roughly offset by root replacement, unless other stresses tip the balance in favour of acute disease or towards progressive decline. Chronic *Phytophthora*-related disease can be very difficult to detect and, when it is part of a disease complex involving climatic episodes or other environmental factors, very difficult to diagnose. Moreover, primary and recurrent *Phytophthora* root damage is likely also to predispose trees to attack by other organisms, such as *Armillaria* or bark beetles. By the time such events are investigated, the causal *Phytophthora* may have all but disappeared.

EUROPE BEFORE 1990

3. Until the beginning of the 1990s, concern about Phytophthoras on trees in Britain was focused mainly on sporadic mortality of sweet chestnut *(Castanea)* and beech on heavy clay soils, resulting from root and collar necrosis ('ink disease') caused by *P. cambivora* and *P. cinnamomi*[1]. Significant mortality has also occurred periodically across a wide range of trees and woody ornamentals *(Aesculus, Tilia, Prunus, Taxus, Chamaecyparis, Abies, Rhododendron* and *Erica)*, the cause usually being *P. cambivora, P. cinnamomi*, or one of four or five other *Phytophthora* species[2,3]. Lawson cypress *(C. lawsoniana)* is especially susceptible to *P. cinnamomi*, and there has been steady mortality of this species in garden centres, parks and gardens across the south of England since a mini-epidemic during the 1960s–70s. A number of Phytophthoras also cause mortality of conifer and

hardwood seedlings (particularly beech) in nurseries, while in Christmas tree plantations, young Douglas fir and noble fir are susceptible to *Phytophthora* on poorly drained sites.

4. Much the same picture has occurred across Europe, but with one notable exception. This is the major losses that occurred among stands of sweet chestnut in Italy, Spain and Portugal during the 1920s–1940s. Although, this epidemic was initially attributed to *P. cambivora*, it was probably also due to the spread of *P. cinnamomi*[1,4]. Both *P. cinnamomi* and *P. cambivora* are believed to be introduced to Europe. *P. cinnamomi* is probably native to the Papua New Guinea – Celebes area of the south-west Pacific, from where it has been spread to many parts of the world, by man, during the past two centuries. European chestnut (like Lawson cypress, Douglas fir and yew) is highly susceptible to *P. cinnamomi* when soil conditions favour infection. Moreover, unlike many Phytophthoras, *P. cinnamomi* has an enormous host range (>1000 species to date[5]). Why this is so is not yet known. Possibly *P. cinnamomi* produces a specialised toxin that is tolerated by its natural hosts in its native home, whereas the many other hosts that the pathogen encounters elsewhere have little resistance to it. Indeed, there is some evidence that the pathogen may produce a toxin that affects the host's stomatal activity, mimicking the effects of drought.

PHYTOPHTHORA ACTIVITY WORLDWIDE

5. Other major disease episodes have occurred outside Europe. In North America, the arrival and spread of *P. cinnamomi* earlier in this century led to a destructive epidemic on native American chestnuts and their relatives in the lower Mississippi valley area. The fungus spread steadily from valley bottoms up the hillsides, killing most trees as it spread[6]. In the Pacific northwest, first *P. cinnamomi* and then *P. lateralis* have invaded the native stands of Lawson cypress in southern Oregon and northern California, where it is a large timber tree. There, *P. lateralis* has been spread in infested soil carried by forest machinery and on the feet of humans and animals. It has also been spread via water run-off along affected ditches and watersheds. As a result, Lawson cypress is now considered a threatened species within its native region. In some areas, strict quarantine regulations are now in force[7].

6. In Australia, *Phytophthora* is recognised by Act of Parliament as one of the 'Four major threats to the Australian Estate'. Of particular concern has been the spread of *P. cinnamomi*. Initially, attention was focused on the death of jarrah *(Eucalyptus marginata)* forest and much of the associated shrubby understorey in Western Australia[8], and on a similar mortality of dominants and understorey in the Brisbane ranges in the east. Again, the fungus was often introduced to new areas by forest machinery and road building equipment. Unfortunately, the pathogen has also spread into world heritage 'Gondwana origin' ericaceous and proteaceous heath communities on the hills and sand plains of south-west Australia. Here, there can be as many as 400 different plant species per square kilometre, and 60–80% of this spectacular flora is susceptible to the fungus[9]. Disease fronts are often clearly visible from the air. *P. cinnamomi* is also invading and killing elements of the internationally renowned 'Fejnbos' woody heath vegetation of Cape Province, South Africa, which shares many botanical relatives with Western Australia.

EUROPE SINCE 1990

7. Since 1990, the profile of Phytophthoras in forests and natural ecosystems has been rising in Europe. In 1992, a widespread decline and mortality ('sudden death') of deciduous oaks, (Figure 1; mainly holm oak, *Quercus ilex* and cork oak, *Q. suber*) in the oak forests and savannahs of south-west Iberia was shown to be associated with the presence of *P. cinnamomi*[10]. Since the 1940s, the fungus may well have moved from the highly susceptible chestnuts on to the more resistant oaks[4]. The disease appears to involve interactions between several factors, including exceptionally severe summer droughts since 1980, and unseasonable late summer rains which may have enhanced the activity of *P. cinnamomi*. These factors may have been further exacerbated by changes in land use – from traditional agroforestry with grazing to intensive under-planting with cereals[11]. Many species of the oak forest understorey, such as *Cistus, Lavendula* and *Arbutus*, are also susceptible to *P. cinnamomi* (A.C. Moreira, unpublished observations). The situation in Iberia therefore has elements in common with that in parts of Australia.

8. *P. cinnamomi* is most pathogenic at temperatures of 25°C and above and does not survive freezing conditions in the soil[8]. The present activity and

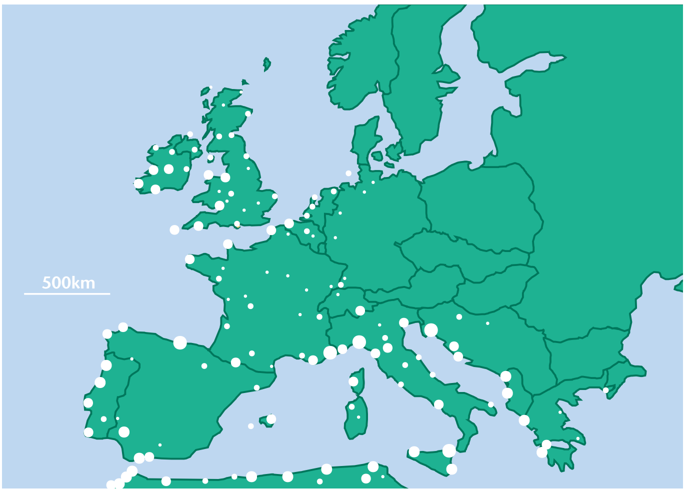
Figure 1 Sudden death of holm oak, *Quercus ilex* associated with root infection by *Phytophthora cinnamomi*. Toledo Province, Spain 1992.

distribution of the pathogen in Europe, therefore, is probably constrained by both summer and winter temperatures. To assess the possibility that the activity of the pathogen in Europe could alter as a result of climate change, a series of computer models has been run. These indicate that with the currently predicted moderate climatic warming up to the year 2050, activity of *P. cinnamomi* is likely to increase significantly in the Mediterranean region and in maritime climates such as that of coastal western Britain, but not in central Europe[12] (Figure 2). However, it should be noted that the extent of the pathogen's activity will also depend upon availability of suitable hosts and other ecological factors[11].

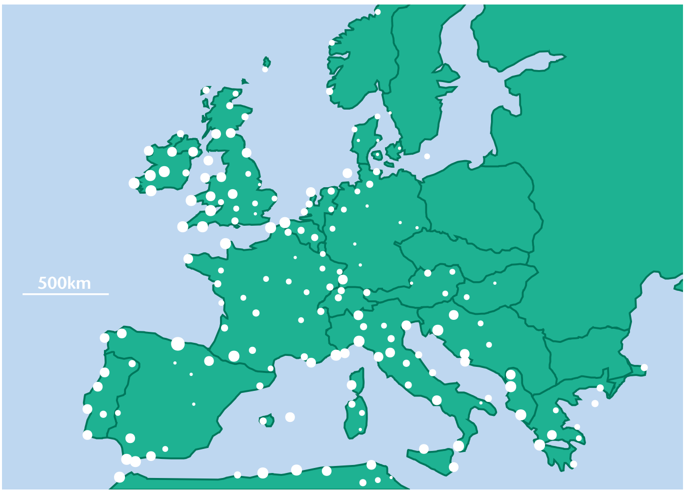
9. There has been a history of recurrent, severe decline of deciduous oaks, *Q. robur* and *Q. petraea*, across central Europe from the UK to Romania, since the 1920s[13-16] (c.f. Figure 3). The discovery that *P. cinnamomi* was involved in Mediterranean oak declines led to a proposal that Phytophthoras could also be involved in this problem[4]. Research carried out in Germany to test this hypothesis has led to the discovery of several *Phytophthora* taxa on diseased feeder roots, some previously unknown[17,18]. At least one of these, *P. quercina* sp. nov.[19], appears to be specific to oak. It also produces a toxin that causes rapid yellowing of leaves. Current evidence suggests that in many *Phytophthora*-associated pockets of oak decline on non-acid soils across central Europe (>pH 4.0), crown dieback levels are correlated with the loss of feeder roots due to *P. quercina* or other Phytophthoras (H. Blaschke, T. Jung and W. Oswald, unpublished observations). Isolation of some of these

Figure 2 Activity of *Phytophthora cinnamomi* in Europe as predicted by a computer model. Activity of *P. cinnamomi* is indicated by the relative size of the dot.

a. Activity under current or 'normal' climatic conditions. This represents a good fit to the known activity of the pathogen, including its occurrence as an oak dieback pathogen in southern Spain and Portugal and its sporadic activity in southern Britain.



b. Activity assuming a 1.5°C increase in mean annual temperatures – a current climate change prediction for around the year 2050.



c. Activity assuming a 3°C increase in mean annual temperatures – a current climate change prediction for around the year 2100.

Figure 3 Healthy (right) and declining (left) pedunculate oak, *Quercus robur*, Hampshire, UK. 1998.

new Phytophthoras is difficult, requiring specialist techniques[19]. This could well account for their not having been discovered previously. It remains to be demonstrated whether they are endemic, i.e. a natural component of deciduous oak ecosystems, or introduced organisms.

10. Another development in Europe is the discovery of a new Phytophthora disease of *Alnus* spp., in particular of the common riparian alder, *A. glutinosa*. The disease, a root and collar rot which can result in rapid girdling of the stem (Figure 4), was first diagnosed in Britain in 1993 by the FC disease diagnostic and advisory service, Alice Holt. It has since been shown to be widespread across Britain, spreading along river systems and also into some orchard shelterbelts and woodland plantings[20,21]. It is also present across much of Europe from Sweden to France, in some areas causing much local mortality. The *Phytophthora* involved is specific to alder. It also exhibits a number of very unusual genetical and developmental features[22] and appears to be a still evolving swarm of interspecific hybrids[23]. The emergence of the hybrids may be a result of man's commercial activities, bringing together *Phytophthora* species that were previously geographically isolated from each other[23].

11. The involvement of *Phytophthora* root pathogens in current oak declines, the possibility that the activity of some Phytophthoras may increase with global warming, and the continuing discovery of previously unknown tree-infecting Phytophthoras including some that are both new and evolving has led to pressure for increased research and collaboration on this group of diseases across Europe. Several co-operative projects (EU and NATO) have been undertaken on the role of *P. cinnamomi* in Mediterranean oak decline. Similar European-wide projects are now underway on the role of Phytophthoras in deciduous oak decline, in chestnut mortality and in alder mortality respectively. The FC's research contribution includes a preliminary survey for the presence of root infecting Phytophthoras at oak decline sites in Britain already with 'positive' results, including the isolation of *P. cambivora* and *P. quercina* from a wide geographic range of sites; testing of pathogenicity of these Phytophthoras to oak and other hardwoods; investigating the spread, impact and management of the Phytophthora disease of alder along Britain's rivers; and studying the origins of the new alder *Phytophthora* and how it is still evolving into new pathogenic forms. As a result of increasing worldwide interest, a new IUFRO (International Union of Forest Research Organizations) Working Group on Phytophthora diseases was set up in 1998 to co-ordinate research and information internationally.

12. Although Phytophthoras are aggressive pathogens, they are also seasonally active, delicate ephemeral organisms that are quickly replaced in host tissues by other fungi and by bacteria. They are therefore often difficult to isolate for diagnosis, for taxonomic identification or for quarantine tests. Isolation of

Figure 4 Characteristic 'tarry spots' or stem flux on the trunk of an alder girdled at the collar by the new alder *Phytophthora*.

P. cinnamomi or the alder Phytophthoras by traditional, expensive and highly time-consuming 'baiting methods' (which rely on attracting zoospores to vegetable baits) is usually only 10–20% successful even from fresh, active bark lesions. For *P. quercina*, isolation success rates can be even lower. In consequence, the activity of Phytophthoras in forest ecosystems may have been underestimated. More effective diagnostic tools are therefore needed, including tools that will reveal changes in population levels of these pathogens. Genetic fingerprinting methods (so called PCR-based diagnostics, which use DNA sequences) have recently been developed in a number of European forest pathology labs. These methods enable rapid diagnosis of *Phytophthora* species in newly infected host tissue. They may eventually also allow their detection in old infected plant material or in infested soil, and promise to be far more accurate and efficient than traditional survey and isolation procedures.

13. Even when successfully isolated into pure culture, Phytophthoras are often difficult to identify to a species. Their sporing structures are difficult to obtain and there is often overlap in spore shape and size between species. Indeed, certain traditional, long standing morphological species in the genus *Phytophthora* have recently been shown to contain multiple, behaviourally distinct species[24]. The new alder *Phytophthora* exemplifies the problem. Morphologically, it closely resembles *P. cambivora*, and has been labelled as such in several culture collections. Yet, it is a unique taxon with a different sexual system, different genetic structure and unique behaviour[22]. The latter includes its being very aggressive and host-specific to alder, whereas *P. cambivora* is non-pathogenic to alder. Meaningful and effective international quarantine protection for our forests depends on overcoming such taxonomic problems. This is most likely to be achieved by combining the use of DNA fingerprinting techniques with the use of behavioural and morphological characters, such that species units in *Phytophthora* can be correctly and accurately defined[23]. With this in mind, the FC is involved in a collaborative project with the Scottish Crops Research Institute, Dundee with the aim of amassing DNA fingerprints characteristic of Phytophthoras associated with trees. This information may be used both in disease diagnosis and in species identification. It represents the arrival of a new, molecular era of disease diagnosis, not only for Phytophthoras but for all infectious diseases of trees.

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