The Ever-increasing Threat from *Phytophthora* Pathogens in Europe©

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***Phytophthora* species are almost exclusively plant pathogens and *Phytophthora infestans* (potato blight pathogen) can be regarded as quite unrepresentative of the genus since the majority of the recognized species are virulent pathogens of plant roots rather than of aerial parts. *Phytophthora* pathogens are now the main risk to woody ornamental, fruit, and forest crop plants. The range of known phytophthora diseases continued to expand in Europe throughout the last century not just in an extension of the host ranges of well recognized pathogens such as *P. cinnamomi* but in an alarming arrival of previously unknown species such as *P. ramorum* and the alder phytophthora, within the last decade. The common features of these diseases are their absolute requirement for water, their great survival ability, and the lack of any realistic chemical eradication possibilities. The most reliable management practices are isolation, thorough attention to plant and soil hygiene, vigilance as regards the origin of planting material, and the destruction of infected plants. In many cases, except with *P. ramorum*, healthy cuttings can still be successfully taken from infected plants but total elimination of infection from contaminated soils can be achieved only by high temperature treatment. It is likely that the number of *Phytophthora* pathogens causing disease of economic importance will continue to increase.**

INTRODUCTION

Phytophthora infestans, first described in 1876 and the type species of the genus is really quite unrepresentative of phytophthoras in terms of the range of plant diseases caused, since the majority of the 70 to 80 species recognized worldwide are virulent pathogens of root systems rather than aerial parts. There has been a steady increase in the number of species described over the last century and while the number of species in many genera of plant pathogens has been relatively stable in the last 10 years, in the case of *Phytophthora* there has been an alarming increase in the number of authenticated species new to science, and in new and quite unique diseases. In their comprehensive account of *Phytophthora* diseases worldwide, Erwin and Ribeiro (1996) chronicle the identification of species and the plant diseases caused and state that while four species were identified in the late nineteenth century there was a steady increase in the species numbers identified throughout the last century.

Phytophthora species are not regarded as being truly saprophytic (with the possible exception of *P. gonapodyides*) and thus any *Phytophthora* isolated from a plant must be regarded as a disease causing agent.

SYMPTOM DEVELOPMENT AND PATHOGEN BEHAVIOUR IN WOODY PLANTS

Phytophthora species can attack the roots of young seedlings resulting in symptoms similar to damping off but they are best known as causes of root and collar rot in older plants. Development of the diseases is predominantly in the root system (the recent exception being *P. ramorum*) with little progress into the aerial parts though some species can attack seedlings above ground level and then spread down to the root collar.

There are many cases of misdiagnosis of phytophthora attack based merely on symptoms of wilting, stunting, root mass decline or death, any or all of which can result from adverse abiotic factors, infection by other pathogens such as *Armillaria* spp., and insect attack. *Phytophthora* pathogens produce no visible signs of their presence in root and stem attacks and expert diagnosis is required for confirmation. Likewise it is impossible to determine if soil is harbouring survival stages of these diseases by any simple techniques.

Classical symptoms include wilting, yellowing, and retention of dried foliage, darkening of young feeder roots and occasionally the larger roots, reduction of the root mass, and frequently the development of a brown staining in the inner bark and wood. This staining can extend above ground level for some tens of millimetres and is a diagnostic help. The main effect is a result of root malfunction due to destruction of feeder roots and the inability of the plant to adequately absorb enough water and nutrients from the soil, so symptom development will be related to environmental conditions. Symptom expression may be ultimately precipitated by drought conditions but a necessary earlier stage in the disease development will have required moist or waterlogged conditions and relatively warm soils.

A further complication arises as woody plants, particularly when established for a number of years, can tolerate phytophthora infection for many months or even years before the advance of the disease and prevailing environmental conditions precipitate symptom development and the search for a causal agent. The precise mechanisms by which these pathogens destroy functioning roots are still not agreed and range from the production of toxins, macerating enzymes, or simple mechanical disruption of root cells (Erwin et al., 1983).

MYCOLOGY OF PHYTOPHTHORA PATHOGENS

Growth and Dispersal. The mycelium consists typically of coenocytic, branched, hyphae some 10–15 µm wide. The asexual sporangia (20–80 µm diameter) are produced profusely in a film of water on the surface of infected roots and, while these sporangia may be deciduous in some cases, the normal sequence of infection is that swarms of minute swimming zoospores (8–12 µm) are released and these are selectively attracted to susceptible hosts and encyst or attach themselves to and infect fine roots. Further zoospores are produced from repeated generations of sporangia, which can develop within a few days particularly when the soil is moist and warm, and are released into the soil. Consequently zoospore numbers can build up quite rapidly.

Zoospores are flagellate and thus independently motile but their maximum recorded range is no more than 40 mm (Weste, 1983) from their place of liberation from sporangia. Instead, they rely very much on passive movement in water and thus their spread is very dependent on water movement and slope of the substrate. The sporangia and zoospores are easily transported in drainage water, contaminated soil and on tools, footwear, vehicles, and of course in irrigation water if a source is contaminated.

Survival. Two specialised survival spore types are of major significance in the epidemiology of these pathogens: asexual chlamydospores (30–95 µm) and sexual oospores(20–60 µm). These are produced when conditions become unfavourable, either when food from the host source is reduced or when temperature or moisture levels are limiting for vegetative advance of the fungus. When conditions become favourable again they germinate by producing either mycelium or sporangia and the disease cycle resumes. The longevity of these spore forms varies among species but it can be taken that the chlamydospores and oospores are capable of surviving for minimum periods of 5 to 10 years.

Zoospores and sporangia, by contrast, have no relevant long-term survival capacity while mycelium within host tissue can be presumed to survive as long as that tissue remains intact and unaffected by drying or degradation by other organisms. One to 2 years' survival in the root system of recently-killed plants can be anticipated while mycelial survival in infected roots of growing plants is of indefinite duration.

PHYTOPHTHORA SPECIES AS PATHOGENS OF WOODY PLANTS IN EUROPE

Up to the 1990s woody plants in Europe were affected by a relatively restricted number of *Phytophthora* pathogens. We were familiar with a background level of *P. cambivora* on broadleaved species, *P. syringae* and *P. cactorum* as causes of root and fruit problems on apple and the dramatic spread of *P. cinnamomi* in ornamental plants such as *Erica* sp. *Rhododendron* sp. and notably forms of *Chamaecyparis lawsoniana.*

Despite the enormous host range of *P. cinnamomi*, with almost 1000 host species (Zentmyer, 1980), and the reputation that it had for killing great numbers of trees in Australia, New Zealand, and the U.S.A., the disease in Europe seemed to effectively be confined to nurseries. In Ireland and the U.K. reports of losses of woody plants, after planting out, were and still are few. Legislation and a full understanding of the biology of the pathogen effectively limited its spread.

In that period also, *P. eriugena* was described (Clancy and Kavanagh, 1978) causing a stem and collar rot on *C. lawsoniana* in Ireland and this species, quite unusually in woody plants, exhibited oospores in foliage while having little effect on roots.

Since the early 1990s there has been an ongoing change in the spectrum of diseases caused by *Phytophthora* species, and in the genus itself. Scientists have been able to study these changes with the advent of more discriminating molecular diagnostic and comparison techniques. In 1993, Wilcox, et al., confirmed what was then regarded as the phenomenon of a form of *P. fragariae,* recognised as a very specific pathogen of strawberry (*Fragaria* sp.) causing root rot of raspberry (*Rubus* sp.) though the specific disease on raspberry had been recognised in the previous decade and other *Phytophthora* species implicated. The early 1990s also saw greater attention to the damage being caused by *P. cinnamomi* in stands of *Quercus* sp. across southern Europe (Brasier, 1999) while Jung et al. (1996,1999) was the first to describe *P. quercina, P. pseudosyringae, P. uliginosa, P. psychrophila,* and *P. europea* as pathogenic to *Quercus* sp. or associated with its rhizosphere.

The Alder Phytophthora. In 1993, a lethal phytophthora disease of common alder (*Alnus glutinosa)* was identified at several places in the U.K. The disease was subsequently found to be widespread in southern Britain and it was most commonly found in trees growing on or near the banks of rivers. *Alnus incana* and *A. cordata* were also attacked. A European Concerted Action on the disease was established in 1998 and has now reported (Gibbs et al., 2003) on the nature, distribution, biology, and current and potential impact of the disease.

The disease is characterised mainly by thinning foliage in the growing season with individual leaves being abnormally small, yellow, and sparse and, while other features such as abnormally heavy fruiting may be observed, critical features are externally visible dark bark lesions, often basal in origin and discrete tarry spots with rusty exudations. By 2003, alder phytophthora had been isolated in U.K., The Netherlands, Germany, Sweden, France, Austria, Belgium, Ireland (Clancy and Hamilton, 2001), Italy, Hungary, and Lithuania. It had not been found from symptomatic trees in Denmark, Finland, Norway, Poland, or Estonia.

Shortly after the disease was first noted, it was postulated (Brasier et al., 1995) that the causal organism was an unusual form of *Phytophthora cambivora,* a well-known root and stem pathogen on a range of broadleaved trees, though not previously recorded from alder. This new fungus was described as being distinct from *P. cambivora* in its appearance in culture, and in being homothallic. Further work (Brasier et al., 1999) established that the alder phytophthora comprises a range of species hybrids divided into a standard type (which is the predominant type across Europe) and several variant types (unique to particular geographic locations) which are morphologically, behaviourally, and genetically distinct but all with *P. cambivora* and, surprisingly, *P. fragariae* as parents. Thus it is postulated that the alder phytophthoras appear to be a group of recent species hybrids that are still in the process of evolution.

In terms of epidemiology and dissemination, the alder phytophthora can be regarded as typical but with the added disadvantage that the frequent riverside location of the host is an ideal situation for successful disease development and offers little prospect of introducing any disease reduction strategies in affected alder populations. Many cases of this disease can reasonably be attributed to the introduction of diseased planting material and subsequent spread by surface water, irrigation, or flood water. However the disease has also been reported from alder shelterbelts without any logical explanation for its arrival on those sites. However, as is the case with all phytophthoras, one must be alert to the possible unconscious spread by human activity or on the root systems of non-hosts.

Phytophthora ramorum. Throughout the last decade, a new twig and foliage blight of *Rhododendron* sp. was noted in European countries, killing both mature trees and nursery plants. The associated pathogen was identified as a *Phytophthora* species and though it had similarities with *P. lateralis* and *P. palmivora* it was regarded as a new species and named *P. ramorum* in 2001 (Werres et al., 2001). It was also found on *Viburnum* sp. and *Camellia* sp. At the same time, a lethal canker disease of oak in the U.S.A., which came to be known as "sudden oak death", was under investigation and it was also concluded to be caused by *P. ramorum*, though it is now believed that the species exists in a number of forms, which differ in their host range and pathogenicity. In North America, the disease has also now been found not only on oak but also on other broadleaved trees, on a number of conifers and on a broad range of wild and planted ornamental species across many plant families (Rizzo and Garbelotto, 2003). *Phytophthora ramorum* is therefore a pathogen attracting much interest across Europe where records of its occurrence, in at least 10 countries, continue to expand, not only on ornamental species from nurseries and retail outlets but also recently, in 2003, confirmed from *Pieris* sp., mature beech, horse chestnut, and two oak species in the U.K.

It can be shown experimentally that the American and European *P. ramorum* isolates are both capable of infecting a number of European tree species. However it is believed that the natural European and North American populations of *P. ramorum* differ in a number of respects and thus the European and U.S.A. outbreaks are probably unrelated, and widespread devastation of oak in Europe will not result from the current European forms of *P. ramorum*. Nevertheless emergency measures against the introduction and spread of *P. ramorum* and a monitoring programme were introduced throughout the E.U. from November 2002.

On *Viburnum* and *Rhododendron* the characteristic symptoms range from dieback of shoots to elongated brown to black lesions on stems, which can be described as canker lesions with the discolouration extending through the bark and into the wood. Leaf lesions are brown to black spots, typical of many leaf spot type diseases. In all cases, isolation of the pathogen is required for positive diagnosis, though the production of sporangia can occur on plants, in situ, and could aid in a preliminary diagnosis. On oak and other tree species the main symptom which ultimately leads to the decline and death of the host is a stem canker where the pathogen can invade phloem, cambium, and xylem with major disruption, occasionally producing black or tarry weeping bark lesions but more commonly open cankers exposing the wood. It is significant that in the case of this disease the pathogen does not normally extend to the root system of infected plants.

A major difference, compared to the normal broad range of *Phytophthora* sp. affecting woody plants, is that the sporangia which are morphologically typical of the genus are deciduous and accepted as having major involvement in aerial spread of the pathogen, predominantly in water droplet or mist borne movement rather than being truly air dispersed. Survival in this species is predominantly as mycelial infections in host tissues but it is well equipped with chlamydospores, formed abundantly in culture on individual isolates and possibly in natural situations too. While the other long-term survival structures, the sexual oospores, have been induced in laboratory pairings, individual isolates will not produce them and thus are not as yet anticipated in nature.

***Phytophthora* Pathogens in Christmas Tree Crops.** In Ireland, apart from the detection of *P. ramorum* and the alder phytophthora we have seen increased pathogenic activity of *Phytophthora* species in Christmas tree plantings of noble fir (*Abies procera*). *Phytophthora cinnamomi, P. cryptogea, P. cambivora, P. megasperma*, and *P. undulata* were reported by Shafizadeh and Kavanagh (1999) while, in 2002, Anacker and Clancy (unpublished) recorded *P. cactorum, P. cambivora, P. cinnamomi, P. citricola, P. cryptogea, P. dreschleri, P. gonapodyides, P. megasperma* and *P. pseudotsugae* from that host. These findings are disturbing since it was assumed that development of *Phytophthora* species on noble fir plantations were most likely to arise from introduction of contaminated material, which was a clear probability in some, but not all, cases.

THE CAUSE OF THE INCREASED PHYTOPHTHORA RISK

One might speculate that modern diagnostic and comparison techniques might amalgamate rather than further separate taxa, but modern techniques reinforce and confirm the noted expansion of the number of known phytophthoras.

There are two likely explanations for the emergence of new species and forms of *Phytophthora* and new diseases and host ranges resulting from increased activity of new or established species:

- The bringing together of closely-related specific pathogens, which had been previously isolated geographically, as a consequence of increased plant trade within and between regions, leading to opportunities to hybridise (Brasier, et al., 1999)
- Changes in climate resulting in increasing prevailing temperatures — many *Phytophthora* species are of tropical or subtropical origin (Brasier and Scott, 1994)

MANAGEMENT OF PHYTOPHTHORA DISEASES

At present there is no one simple method for management of *Phytophthora* pathogens. Minimising the risk consists of understanding the high risk plants and situations; thorough plant hygiene; careful plant location; environmental management, and generally good husbandry practices.

Until the advent of *P. ramorum* one could confidently accept that cuttings taken from aerial parts of phytophthora-infected woody plants could be healthy, provided the extent of lower stem infection was established and contamination of the aerial plant from the substrate had been avoided but this clearly does not apply in the case of *P. ramorum*.

The addition of organic matter to soils is also often suggested to retard the activity of *Phytophthora* through the stimulation of antaganostic and competitive bacteria and saprophytic fungi but true biological control is still an aspiration.

Many very effective chemicals are currently used in the management of *P. infestans* on potato and other crops but these materials and techniques are largely irrelevant and uneconomic in attempting to manage diseases of woody plants where the infection will probably be within the stem or root tissues rather than in foliage. It is possible that chemicals may yet have a protectant role in relation to *P. ramorum* on ornamental species if regulatory and hygiene measures fail to control that disease. Spraying or drenching plants with potassium phosphonate or other phosphonate preparations has had success in slowing the progress of some phytophthoras, particularly in fruit crops where it may be important to salvage a season's crop, but this practise will not eliminate the pathogens from an infected root system or rhizosphere. Nothing short of complete heat or chemical sterilisation will kill these pathogens in soils or roots. Short term application of chemicals is likely to add to the phytophthora problems rather than solve them, by suppressing but not eradicating infection.

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