beetle infestation. These treatments require the use of chemicals with a relatively broad spectrum of action and should be used sparingly and only in high-value landscape situations.

See also: **Entomology**: Bark Beetles. **Pathology**: Diseases of Forest Trees; *Phytophthora* Root Rot of Forest Trees. **Tree Physiology**: Root System Physiology; Stress.

Further Reading

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Phytophthora Root Rot of Forest Trees

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Introduction

As a genus *Phytophthora* can be considered as the most devastating group of plant pathogens on earth. Members of the genus cause huge economic losses in agricultural crops annually and are extremely destructive in a range of forest ecosystems worldwide. Their direct affect on plant losses is really quite well documented. The genus name is aptly derived from the Greek that means *phyto* (plant) and *phthora* (destroyer). There is still much debate over the taxonomy of *Phytophthora* and there are over 64 species, but this constantly changes with new species being described and others amalgamated as molecular diagnostics tools are used to characterize the genus. Some species such as *P. cinnamomi* have a wide host range whilst others have one to only a few hosts, consequently as a genus it is extremely plastic in terms of the range of plant species it impacts on. This article will provide a general but not a comprehensive overview of the major *Phytophthora* diseases of forest trees and cover impacts, threats, and methods of control.

Life History

The genus belongs to the class Oomycetes in the Kingdom Chromista and is more closely related phylogenetically to the heterokont algae than the true fungi or Mycetae. Oomycetes are diploid, have a coenocytic thallus or mycelium, and they reproduce asexually to produce chlamydospores or by the production of sporangia. Chlamydospores are formed terminally at tips of hyphae or are intercalary. They can be thin- or thick-walled and function as survival spores. Sporangia or more correctly zoosporangia are produced under warm and moist conditions from specialized hyphae or sporangiophores. The sporangia can germinate directly to produce a germ tube or indirectly to produce uninucleate, biflagellate zoospores within the sporangium. The zoospores emerge from the sporangium into a temporary vesicle that rapidly breaks, allowing the zoospores to swim away. The zoospores are propelled by two flagella; one is a long whiplash and the other a shorter tinsel. The zoospores can remain motile for hours and are attracted chemotactically to substrates where they encyst. The cysts germinate to produce a germ tube and if appropriately located will invade living organs of susceptible plant species to cause disease.

The sexual structures of *Phytophthora* consist of an oogonium (egg-containing female component) and an antheridium (male component). Reduction division (meiosis) of the chromosomes from the diploid to haploid in nuclei occurs in the coenocytic antheridium and oogonium (**Figure 1**). Sexual reproduction occurs when a fertilization tube from the antheridium deposits its nucleus inside the oogonium, fusion between the two nuclei occurs, and an oospore forms within the oogonium. Oospores like chlamydospores are survival spores and under suitable environmental conditions will germinate to produce single to multiple germ tubes at the tips of which sporangia can

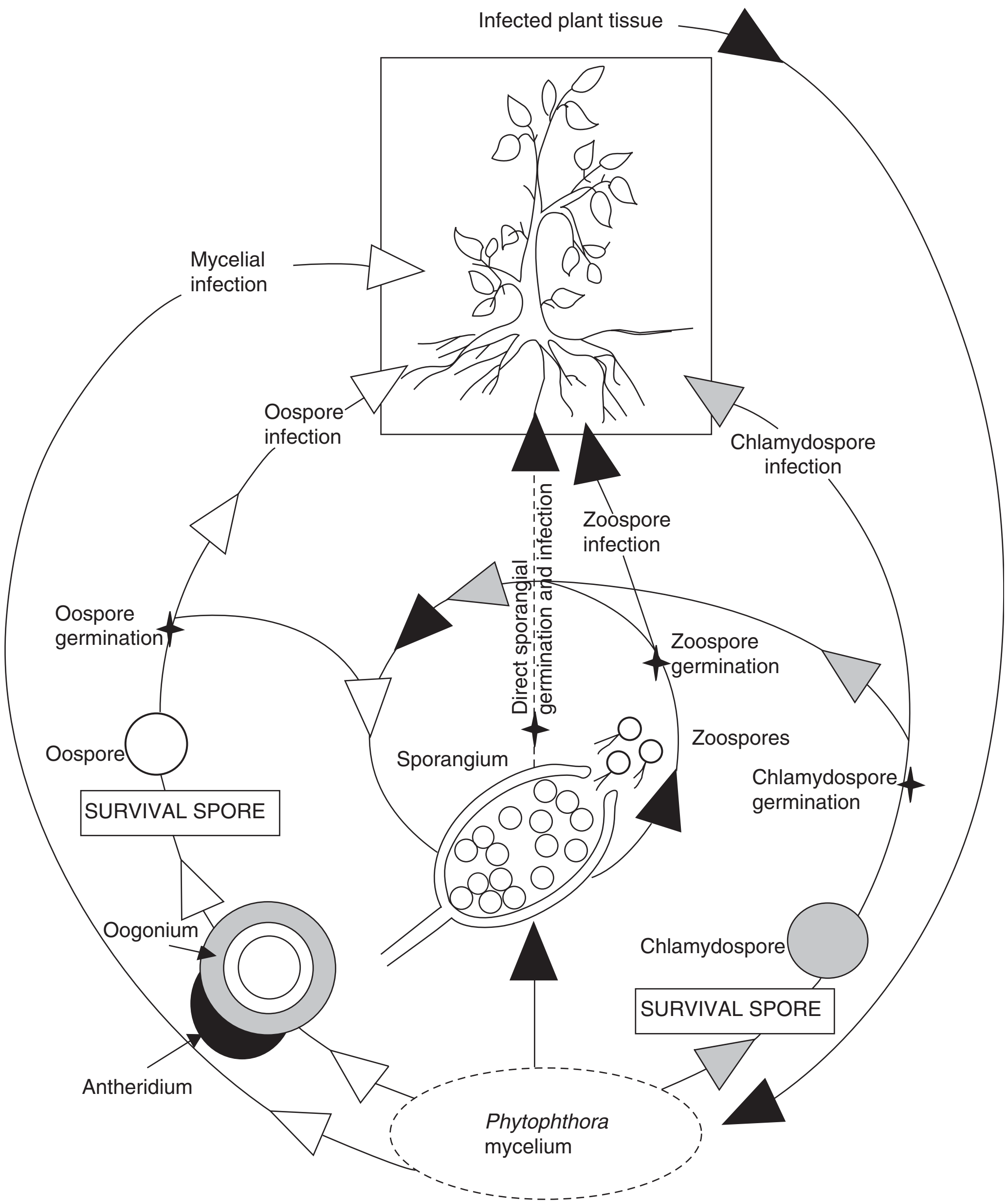

Figure 1 *Phytophthora* life cycle and infection strategies.

form. However, in some self-fertile (homothallic) species, oospores can be important sources of dissemination, germinating rapidly to produce sporangia under optimum conditions.

Phytophthora species are either homothallic or self-sterile (heterothallic). In the heterothallic species two compatible mating types must make contact before oospores will form at the point of contact between the two. In heterothallic species, the crossing of compatible (A1 and A2) mating types is likely to be the source of new races or biotypes, whilst in homothallic species, oospores function as survival propagules in plant debris.

The above characteristics of *Phytophthora* make it unique among pathogenic fungi since members within this genus are able to initiate and cause disease on nearly all parts of the host plants. In forest trees this includes the roots and collars (e.g., *P. cinnamomi*) and foliage (e.g., *P. ramorum*).

Spread

It is highly likely that many phytophthoras have been spread between countries and continents since the European settlement of the Americas, Australasia, Africa, and other countries. This would have occurred in the soil of containerized horticultural and ornamental trees being transported between countries. For example, *P. cinnamomi* was likely to have been introduced on planting stock into Australia on one of the first sailing ships from Europe. More recently, as trade barriers break down within the European Union, less stringent quarantine regulations will certainly provide avenues for the transfer of different *Phytophthora* species between regions. This introduces *Phytophthora* species to new hosts that previously have had no contact with a particular *Phytophthora* species and/or alternatively allows sexual reproduction to occur between compatible species allowing for new hybrids to develop. The latter is a likely scenario for the alder phytophthoras (see below).

Once in a region, phytophthoras can be spread through the movement of soil on vehicles, heavy earth-moving equipment, on the feet of hikers, feral or wild animals, surface water flow, and infested nursery stock. Consequently, once phytophthora are present, autonomous spread and spread through the movement of vehicles, people, and animals are extremely difficult to control.

Symptoms

In susceptible trees, many types of symptoms are observed and these depend on the *Phytophthora* species and the host species being colonized. In many trees, primary invasion is through the small absorbing roots and causes brownish to black firm roots with little progression into the larger lateral roots. In this case decline and death tends to be gradual and often associated with other predisposing biotic or abiotic factors. In other hosts, *Phytophthora* invades the lateral roots and colonizes the phloem girdling the roots and frequently moving up into the collars of the tree, where cankers are produced. Cankers can cause cracking of the stem or trunk, bleeding or exudation of kino or red sap, often with entire girdling of the trunk, leading to a restriction of transpiration, followed by tree death.

In broadleaved trees, invasion results in a gradual deterioration of the crown, with chlorosis, reduction in leaf size, absence or reduced new growth, wilting of leaves, and dieback of small branches usually being the first symptoms. These are followed by the development of epicormic shoots on large branches, which over time will die back resulting in a gradual decline leading to the eventual death of the host, although in highly susceptible hosts death can be extremely rapid.

In conifers, wilting does not usually occur and in 'littleleaf' disease of pine, for example, the first symptoms are yellowing of the foliage and needles that are smaller than usual; thereafter shoot growth decreases. In many tree species, decline can be slow and trees do not die until many years after infection.

Predisposing Factors

As with all plant diseases the key components of the *Phytophthora* disease – host, pathogen, environment, and time – are all necessary for a disease to occur. In the absence of the pathogen or a susceptible host disease will not occur. *Phytophthora* species generally require moist and warm conditions in order to cause disease; if these conditions are not present or present for too short a time, again disease will not occur. Consequently, it is critical to understand these factors when considering the biology, ecology, and pathology of a *Phytophthora* pathogen and the diseases it causes. For example, oak decline in Europe and adjacent parts of Asia has been associated with a variety of *Phytophthora* species (**Table 1**).

However, oak decline is also recognized to be a multifactorial disease syndrome with predisposing factors (e.g., industrial pollution, climatic extremes, and inappropriate site), inciting factors (e.g., drought, frost, waterlogging, insect attack, soil nutrient characteristics), and contributing factors (e.g., secondary pathogens) all contributing to decline in certain circumstances. Therefore, predisposition can and does play a role in disease syndromes associated with *Phytophthora* species. A predisposing factor such as drought will frequently speed up death of infected plants.

Phytophthora cinnamomi in Australasia

Over 31 *Phytophthora* species have been associated with plant deaths in Australia. The majority of these are horticultural, agricultural, or nursery pathogens with only *P. cinnamomi* causing major losses to forest trees. The loss of floristic and structural diversity, and consequential effects on faunal diversity are now considered a major problem of ecosystem breakdown and economic loss. As a result, *P. cinnamomi* has been listed as a 'key threatening process' to Australia's biodiversity in the Commonwealth's Environment Protection and Biodiversity Conservation Act 1999. *Phytophthora cinnamomi* is one of 11 key threatening processes and the only microorganism listed.

The major impact and threat is to open forests, woodlands, and heathlands of southern Australia. Its impact has been likened to that of the last ice age by botanists. For example, in the southwest of Western Australia alone it affects over 2000 of the approximately 7000 native plant species, of which 3000 are

Table 1 *Phytophthora* species isolated from some forest trees worldwide[a]

Host	Alder *Phytophthora*	*P. cactorum*	*P. cambivora*	*P. cinnamomi*	*P. citricola*	*P. cryptogea*	*P. drechsleri*	*P. ereugena*	*P. europaea*[b]	*P. hibernalis*	*P. inundata*	*P. lateralis*	*P. megasperma*	*P. nicotianae*	*P. syringae*	*P. gonapodyides*	*P. psychrophila*[b]	*P. quercina*	*P. ramorum*	*P. uliginosa*[b]
Acer macrophyllum																			+	
Acer sp.			+		+								+							
Aesculus hippocastanum											+									
Alnus cordata	+																			
Alnus glutinosa	+																			
Arbutus unedo				+																
Banksia spp.				+	+	+	+													
Castanea sativa		+	+	+	+											+				
Chamaecyparis lawsoniana						+				+		+								
Crataegus sp.																				
Eucalyptus marginata				+																
Eucalyptus seiberi				+																
Eucalyptus smithii														+						
Eucalyptus macarthurii														+						
Fagus sylvatica					+															
Fagus spp.			+																	
Lithocarpus densiflorus																			+	
Malus spp.			+																	
Nothofagus spp.				+	+	+							+							
Pinus echinata				+																
Pittosporum undulatum																			+	
Pseudotsuga menziesii				+															+	
Quercus agrifolia																			+	
Quercus cerris		+	+	+	+											+		+		
Quercus chrysolepis																			+	
Quercus ilex				+														+		
Quercus kelloggii																			+	
Quercus frainetto				+																
Quercus parvula var. *shrevei*																			+	
Quercus petraea				+	+				+								+	+		+
Quercus peduncularis				+																
Quercus pubescens				+																
Quercus glaucoides				+																
Quercus robur		+	+	+	+				+						+	+	+	+		+
Quercus rotundifolia				+																
Quercus rubra				+												+				
Quercus salicifolia				+																
Quercus suber				+			+													
Rhamnus purshiana																			+	
Rubus spectabilis																			+	
Salix matsudana (UK)											+									
Sequoia sempervirens																			+	
Taxus baccata				+	+	+														
Taxus brevifolia												+								
Thuja plicta					+	+														
Toxicodendron diversilobum																			+	
Umbellularia californica																			+	

[a]This list of *Phytophthora* species and hosts is not intended to be comprehensive but rather indicative of the number of each involved in tree decline and death.
[b]*Phytophthora* species isolated from soils in association with forest trees; pathogenicity still to be ascertained through further testing.

endemic; a number of these are important woodland or forest species.

On infested sites, resistant species that replace susceptible plant species tend to be wind-pollinated and do not produce nectar or nutrient-rich pollen and, therefore, do not attract or provide food sources for birds or smaller animals. Regeneration of such sites with susceptible species may never occur if seed reserves are lost; consequently many birds and animals may be lost from infested sites.

Phytophthora cinnamomi in the Americas

Phytophthora cinnamomi has been introduced into most forested regions of the western hemisphere and elsewhere in the world, where it has considerable impact in a range of forest species. It caused significant and catastrophic deaths of American chestnut and related *Castanea* species in forests and woodlands in the USA and removed much of the chestnut from the southern Appalachian foothills. Deaths were first reported in the early 1820s and it was not until 1932 that *P. cinnamomi* was associated with dying chestnut. Together with *Cryphonectria parasitica*, *P. cinnamomi* has essentially removed American chestnut from this region. *Phytophthora cinnamomi* is also the cause of 'littleleaf' disease in shortleaf pine (*Pinus echinata*), where it has caused decline across much of the tree's range in the southern USA. Unlike its association with *Castanea* and the many plant species in Australia where it attacks the main root system and stems of trees, *P. cinnamomi* is a fine feeder root disease in shortleaf pine. It plays a central role in 'littleleaf' disease as it causes severe fine root mortality, predisposing trees to other biotic and abiotic influences that contribute to the disease syndrome.

Phytophthora cinnamomi also causes the decline and death of oaks in Mexico. Although widespread in forests in the Pacific Northwest, *P. cinnamomi* does not impact severely if at all on many susceptible tree species since it is too cold in the wet winters and too dry in the hot summers for it to cause disease. This indicates the importance of the interactions of disease factors for disease to occur in the presence of the pathogen.

Phytophthora cinnamomi and other *Phytophthora* spp. in Europe

Phytophthora cinnamomi has been associated with oak decline throughout Europe and the Mediterranean region, and of all the *Phytophthora* species associated with oak, it is the most devastating. Oaks affected include *Q. cerris*, *Q. frainetto*, *Quercus ilex*, *Q. petraea*, *Q. pubescens*, *Q. pyrenaica*, *Q. robur*, *Q. rotundifolia*, *Q. rubra*, and *Q. suber* (**Table 1**). In Europe, the oak decline phenomenon is a complex disease with predisposing, inciting and contributing factors also contributing to the decline syndrome. *Phytophthora cambivora*, *P. citricola*, and *P. quercina* have also been associated with fine feeder root disease of oaks in Germany and are probably involved in oak decline, although their precise roles are still to be determined.

A total of 13 *Phytophthora* species has been recorded in Europe, with *P. cambivora*, *P. citricola*, and *P. quercina* being widespread. Frequently, *P. cinnamomi* and *P. cryptogea* are restricted to warmer climatic regions of Europe, *P. europaea*, *P. gonapodyides*, and *P. uliginosa* to wet sites, *P. pseudosyringae* sp. nov. to acid sites. There are infrequent isolations of *P. cactorum*, *P. megasperam*, *P. psychrophila*, and *P. syringae*. *Phytophthora* species are certainly associated with oak decline. However, more research is required to understand fully their interactions with abiotic and other biotic factors.

Phytophthora lateralis

The ecologically and economically important forest cedar, Port-Orford-cedar (*Chamaecyparis lawsoniana*) endemic to southwest Oregon and northwest California is severely affected by the introduced *P. lateralis*. It rapidly colonizes trees through the fine roots until it reaches the main stem. The pathogen also infects and kills the Pacific yew (*Taxus brevifolia*), but only when it grows in close association with Port-Orford-cedar. *Phytophthora lateralis* was rapidly spread throughout the native range of Port-Orford-cedar along the Oregon coast with road building and logging activities during the 1950s.

The endemic range of *P. lateralis* is still unknown. However, its introduction into Oregon and California before the 1920s, when deaths were first observed, illustrates how unregulated international plant movements in the horticultural trade has resulted in devastating forest tree epidemics. Deaths of Port-Orford-cedar along infested streams are especially high; however, today the impact appears to be less dramatic, as most of the vulnerable cedar stands are already infected.

Most disease management is directed around road management, such as wet season closures, and washing down of vehicles before moving between infested and noninfested areas. These sanitation activities reduce the likelihood of spread by reducing inoculum loads along roads. In addition, the most vulnerable trees growing along roads are removed. Recently, heritable resistance in Port-Orford-cedar has been shown to exist and breeding is a viable strategy to provide resistant planting stock into forest areas where the pathogen is present.

Phytophthora ramorum

Phytophthora ramorum was first described in 2001 from Germany and the Netherlands associated with blight disease in *Pieris* spp., *Rhododendron* spp., and *Viburnum* spp., although the disease caused by this pathogen had been observed since 1993. It is yet to be isolated from oaks in Europe, but pathogenicity experiments under controlled quarantine conditions indicate that a number of forest tree species (**Table 1**) including *Fagus* and *Quercus* species are susceptible to *P. ramorum*. Therefore, the risk to forest species in Europe is great.

In the USA, 'sudden oak death,' a rapid mortality of oaks (mainly tan oak and live oaks) in wildlands and the urban–wildland interface, has been observed since 1994 in the coastal fog belts of southern Oregon and northern California and is also caused by *P. ramorum*. The disease is currently in epidemic proportions in coastal California, covering an area that runs approximately 600 km south to north from central California to southern Oregon. It has a wide host range including a range of tree species (**Table 1**) and shrubs. In the oak family, all the susceptible species belong to the red oaks (section *Lobatae*), whilst so far no white oaks (section *Quercus*) or golden cup oaks (section *Protobalanus*) are found to be susceptible.

In Europe, only the A1 sexual compatibility type has been found which contrasts to the presence of only the A2 sexual compatibility type in North America. The internal transcribed spacer sequences of the European and American isolates are identical. In mating tests, the isolates rarely, if ever, mate together. Consequently, it is unclear whether *P. ramorum* has a normally functioning $A1 \times A2$ outcrossing system. *Phytophthora ramorum* is exclusively aerial in its biology, unlike other *Phytophthora* species that cause disease in forest trees which are predominantly soilborne pathogens. Although recovered from soil and litter, *P. ramorum* has not been observed to cause symptoms below the soil line. It has been recovered from up to 20 m above the ground from stems with no basal cankers. However, it is still not understood how the pathogen has spread so widely, although it is recovered from rainwater indicating its possible dissemination by rain splash and wind-driven rain.

In northern America, the current geographic range of the disease includes a wide range of forest types within the Mediterranean climatic region of California receiving predominantly winter rainfall and with mean annual rainfall ranging from 85 to 200 cm. It is known to have a wide host range which includes members of the *Caprifoliaceae*, *Ericaceae*, *Fagaceae*, and *Lauraceae* and it is likely that other susceptible taxa will be found.

Of concern is the observation from pathogenicity tests that a number of Australian species from a range of families are susceptible to *P. ramorum*; this includes members of *Eucalyptus* spp. (Myrtaceae) a keystone plant genus of many plant communities. Therefore, if introduced into Australia, it is likely to be a major ecological threat to southern Australian forest or woodland ecosystems with a similar climate to California. The risk is real since *P. ramorum* has very recently been isolated from an ornamental *Rhododendron* species on the island of Mallorca (Spain), another Mediterranean environment. Consequently, it is critical that stringent quarantine measures are in place to ensure *P. ramorum* does not enter Australia or other countries where it is likely to be a problem.

Alder Phytophthora

In 1993, a lethal disease of alder (*Alnus* spp.) was observed in horticultural shelterbelts and along rivers in Britain. It was caused by a new *Phytophthora* species that superficially resembled *P. cambivora*, a common pathogen of European hardwood trees. The disease is now found through much of Europe, including Austria, Belgium, France, Germany, Hungary, and the Netherlands. Trees of all age classes are affected and symptoms include small and yellow leaves, tarry spots and exudations, top dieback, and death. The alder phytophthora is hard to isolate as it is considered a primary parasite and is soon replaced by other more opportunistic but secondary pathogens. Therefore, a range of insect pests and other pathogens are frequently isolated from alders but these are probably a result of the alder phytophthora predisposing the trees to secondary invasion.

The alder phytophthora comprises a range of species hybrids, with a common 'standard' alder phytophthora type found throughout much of Europe. The parents of the alder phytophthoras are probable hybrids between two developmentally different phytophthoras: *P. cambivora*, a fast-growing, sexually outcrossing species, and a phytophthora close to *P. fragariae*, a slow-growing, inbreeding and nutritionally fastidious species.

The standard alder phytophthora is extremely difficult to isolate from soil around diseased alder trees; thus its oospores are unlikely to contribute to survival or spread in the field. Local spread along river systems is probably via zoospores and through dispersal of infected alder debris containing healthy mycelium. International spread may have occurred through the distribution and planting of infested nursery stock. The alder phytophthora represents a serious threat to both natural and managed stands of alder and to the stability of riparian ecosystems in Europe and possibly elsewhere if introduced into other countries.

Currently, there are no clearly defined control strategies in place, although early coppicing of diseased trees is being considered. Trials are being established to evaluate whether differences in disease resistance are present within *Alnus* species.

Other *Phytophthora* Diseases

Many *Phytophthora* species have been isolated from the soils under rainforest, temperate forest, and Mediterranean forest plant species and have not been associated with plant deaths. For example, these include *P. katsurae*, *P. megasperma* var. *sojae*, and *P. palmivora* from rainforest in Papua New Guinea; *P. cactorum* in Australia; *P. europaea*, *P. psychrophila*, *P. citricola*, and *P. uliginosa* from under oaks in Europe; and *P. gonapodyides* in Australia, Europe, and North and South America.

Phytophthora gonapodyides does cause significant damage to fine roots of *Castanea* and *Quercus* in Europe; and with further research is likely to be associated with tree declines in Australia and North and South America. However, it is likely that these could become pathogenic as a result of climate change or through the breakdown of quarantine practices. If, for example, new species are introduced into a region it is possible that hybridization between these and existing species could occur resulting in destructive pathogens. This was the case observed for the alder pathogen in Europe.

Impact on Ecosystem Health and Function

Although it is reasonably well understood how different *Phytophthora* species impact directly on plant species, we have very little understanding on how they impact indirectly on ecosystem health and function. For example, we do not fully appreciate how the loss of the litter layer, changed soil-water status, loss of cover to shade-loving plant species, the loss of vertebrate and invertebrate pollinators, and the potential loss of the fruiting bodies of ectomycorrhizal fungi influence the function and health of ecosystems. These indirect effects are likely to be very profound. For example, in Australia, *P. cinnamomi* has been shown to impact adversely on fauna through the loss of habitat and food sources such as pollen, nectar, and possibly fruiting bodies of epigeous and hypogeous macrofungi, many of which are ectomycorrhizal. A number of small marsupial species rely almost totally on fungal fruiting bodies in their diet, so a decline in a fungal host species can result in loss of animals from an impacted environment. In turn, a loss of animals that turn over soil whilst digging for fungi can affect the incorporation of litter into the soil and result in the increased incidence of nonwetting soils. Reduced soil water uptake can result in increased erosion through increased surface water runoff and drought stress.

These are just a few examples of how *Phytophthora* species can impact on ecosystem function and health, and only very recently have researchers started to take a more holistic approach to examine the wider implications of plant diseases caused by *Phytophthora* diseases on communities in general.

Control

Effective hygiene and quarantine measures must always remain the primary methods of control and containment of all forest pathogens. These must include the stringent control of movement of plant material between regions, countries, and continents. The majority of *Phytophthora* diseases in forests today appear to be the result of new introductions into a region. Therefore, it is critical to stop the spread of the pathogen(s) into noninfested areas. Disease management aims to prevent and restrict spread and intensification of the pathogen and to protect and conserve conservation and economic values and includes:

- rating hazard or identifying levels of risk
- assessing risk or analysis of risk at the landscape level
- hygiene procedures
- manipulating conditions to disfavor the pathogen and to enhance host resistance
- education of the public and land managers and users
- appropriate use of research to address questions as they arise.

Chemical Control

Recently, in Australia, phosphonate compounds applied as foliar applications from aircraft, backpacks, or by trunk injection have been extremely effective in reducing the impact and spread of *P. cinnamomi* in forests and natural ecosystems. Control by one trunk injection have been extended beyond 6 years in some forest species and by 2–3 years with aerial applications. Consequently, applications along disease fronts or to plant communities containing rare or threatened plant species can be a viable and effective way of maintaining plant communities.

Phosphonate (also referred to as phosphite), the anionic form of phosphonic acid $(HPO_3)^{-2}$, controls many plant diseases caused by a range of *Phytophthora* spp., even at concentrations *in planta* that only partially inhibit pathogen growth *in vitro*.

Phosphonate is a systemic fungicide that is translocated in both the xylem and the phloem. In the phloem, phosphonate is trapped and therefore translocated through the plant in association with photoassimilates in a source–sink relationship. Phosphonate treatment induces a strong and rapid defense response in the challenged plant. These defense responses stop pathogen spread in a large number of hosts. Phosphonate exhibits a complex mode of action, acting directly on the pathogen and indirectly in stimulating host defense responses to ultimately inhibit pathogen growth. Recent work in the USA has also shown the chemical to be effective on *P. ramorum*.

It is critical to add an adjuvant when applying phosphonate as a foliar application, otherwise efficacy and persistence of the chemical are severely limited. These increase spray coverage by droplet spreading, promoting spray retention, and reducing spray drift, evaporation and wash-off. Care must be taken to ensure adjuvants are not phytotoxic in their own right.

It is important that plants are treated when they are actively growing and not drought-stressed otherwise uptake and distribution of phosphonate is substantially reduced. Rates of application vary significantly between plant species and communities. In Australia, foliar applications to runoff vary between 0.5% and 2.0% ($5–20\,g\,l^{-1}$), whilst aerial applications are normally in the range $12–36\,kg\,ha^{-1}$ applied as ultra-low-volume sprays. Trunk injections vary between 5% and 20% ($50–200\,g\,l^{-1}$) depending on the species to be injected. Phosphonate can cause severe phytotoxicity and plant deaths if inappropriate concentrations are applied; consequently it is important to conduct preliminary trials before applying the chemical to large areas. It is important to note that although the chemical contains the spread of the pathogen *in planta* it does not always kill it. Therefore, the pathogen can still reproduce and disseminate its infective propagules under optimum environmental conditions. Reduced flowering, pollen viability, and seed viability have been observed in some species and more research is required to determine the long-term impacts of these. To date no adverse affects have been observed on mycorrhizal fungi. However, there is some evidence that repeated applications of phosphonate in horticultural situations does select for phosphonate-tolerant isolates of *P. cinnamomi*, and these isolates also appear to be more virulent. In natural ecosystems, where the chemical is applied infrequently it is unlikely that selection for tolerant *Phytophthora* isolates will occur. The main concern is the movement of supposedly 'pathogen-free' container plant stock from nurseries into areas where the pathogen can escape into forested regions. If these contain tolerant *Phytophthora* isolates problems may arise in the future. Irrespective, of these possible drawbacks, phosphonate provides us with a very viable control option for plant species or individual trees of importance whilst alternative control strategies are developed.

Conclusion

Phytophthora as a genus is extremely plastic in terms of genetic and phenotypic variability, pathogenicity, host range, and long-term survival strategies. As exotic pathogens they are devastating in forest and other plant ecosystems as has been observed in Australia, Oregon, Europe, and elsewhere. It is apparent that there are numerous *Phytophthora* species, with many still to be described in forests worldwide. The biology, ecology, pathology, and genetics of the majority of *Phytophthora* species are still poorly understood. However, it is clear that in addition to the presence of a pathogen and a susceptible host, conducive environmental conditions are critical for a *Phytophthora* disease outbreak to be triggered. Often only small shifts in environmental conditions whether biological, chemical, or physical are required to trigger a *Phytophthora* disease event. Therefore, with increasing global movement of humans and their associated plant produce, and climate change through global warming, new outbreaks of devastating *Phytophthora* diseases are likely to occur.

See also: **Pathology**: Diseases affecting Exotic Plantation Species; Diseases of Forest Trees; Root and Butt Rot Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

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Vascular Wilt Diseases

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Introduction

The vascular wilts include some of the most destructive of all tree diseases, in terms of both the scale of the damage and the speed of attack. Vascular wilt diseases mainly occur in angiosperms and only one example in a gymnosperm has been documented. True vascular wilts are caused by fungi, although there are some similar diseases caused by bacteria. Pine wilt disease caused by the pine wood nematode *Bursaphalenchus xylophilus* is covered elsewhere (*see* **Pathology**: Pine Wilt and the Pine Wood Nematode).

The Characteristics of Vascular Wilt Diseases

The fungi that cause vascular wilt diseases are initially restricted to the xylem elements. They can often achieve rapid dissemination within these elements through the passive movement of spores in the transpiration stream. Xylem anatomy can influence this process, with ring-porous genera, such as oaks and elms, that have large, long earlywood vessels which are particularly vulnerable to invasion. Vascular wilt pathogens often grow out from the xylem into the surrounding tissues after the tree has died. This enables them to establish contact with the outside world and, in particular, with insects that can act as vectors for transport to new hosts. Typically, vascular wilt pathogens do not have the capacity to survive long in the tissues of a dead host.

Generally, all vascular wilt diseases display similar symptoms. Leaves and young shoots on one or more branches suddenly wilt and die. If such a branch is cut, a marked discoloration can often be observed in the xylem of the current year. In a severe attack, symptoms can rapidly develop to kill the whole tree. Much still remains to be learnt about the process of pathogenesis. Vascular wilt fungi have the capacity to produce conidia in water-filled xylem vessels without causing cavitation (i.e., the breaking of the column of water). This can lead to rapid dissemination of the fungus throughout the tree in the transpiration stream. However, at some stage cavitation and an interruption to the water flow will occur. Gums, gels, and toxins may also be produced. In some cases the tree responds by producing balloon-like tyloses within the vessels by extrusion from adjacent parenchyma cells.

Ascomycetous fungi (and related mitosporic fungi) are responsible for most true vascular wilt diseases. Important examples are Dutch elm disease (*Ophiostoma ulmi* and *O. novo-ulmi*), oak wilt (*Ceratocystis fagacearum*), black stain root disease of conifers (*Leptographium wageneri*), and verticillium wilt (principally *Verticillium dahliae*). These diseases are discussed separately below.

Fungal Wilt Diseases

Dutch Elm Disease

Dutch elm disease has caused devastation to elms in Europe and North America. It is caused by two different, although closely related, species of fungi: *O. ulmi* and *O. novo-ulmi*. *Ophiostoma ulmi* was responsible for the first epidemic, which began in the