BOREAL ENVIRONMENT RESEARCH 13: 33–41
ISSN 1239-6095 (print) ISSN 1797-2469 (online) Helsinki 27 February 2008

Alien forest pathogens: *Phytophthora* species are changing world forests

Everett M. Hansen

Department of Botany and Plant Pathology, Oregon State University, Corvallis Oregon, 97331, USA

Received 28 Mar. 2007, accepted 9 July 2007 (Editor in charge of this article: Jaana Bäck)

Hansen, E. M. 2008: Alien forest pathogens: *Phytophthora* species are changing world forests. *Boreal Env. Res.* 13: 33–41.

Phytophthora is a genus of aquatic plant pathogens well known as disease agents in agriculture and forestry. They are water molds, Oomycetes, with swimming zoospores and thick-walled resting spores. Many species are benign in coevolved plant communities, but given the opportunity of introduction to new hosts in new environments, new opportunities for dispersal, or unexpected sexual recombination, they are causing dramatic epidemics in forests around the world. *Phytophthora ramorum* (cause of sudden oak death in western North America and also damaging in Europe) provides a current example, dramatically illustrating the potential of these pathogens for rapid ecological (and economic) damage. *Phytophthora cinnamomi* and *P. lateralis* are also alien to Europe and North America but with different epidemiological strategies. By comparing these three related pathogens and the different consequences of their invasions, some predictions for the future of our forests are possible.

Introduction

Forests and woodlands are plant communities dominated by trees. They harbor a major portion of the Earth's biological diversity. Yet everywhere they are changing rapidly, under pressure from diverse sources. Threats range from direct destruction resulting from human population pressure and agricultural conversion, to the mounting physiological and ecological stresses imposed by a rapidly changing world climate.

Exotic, invasive organisms are prominent in most lists of threats to forest health. These include introduced plants that compete with native vegetation for light, water, and other resources, as well as herbivorous insects and mammals that directly reduce leaf area. Plant pathogenic fungi can be considered herbivores. They are numerous and diverse, affecting trees and other forest plants in many ways. Forests evolved with many herbivorous organisms, and the interrelationships, while dynamic and complex, are usually not threatening to the forest ecosystem. Exotic organisms, however, evolved under different conditions and may find new hosts that lack resistance and environments that favor their development at the expense of the forest. In short, they may become invasive. Several species of *Phytophthora* are especially destructive in world forests.

My goals in this review are to highlight the threats posed by alien Phytophthoras, contrasting the ecological consequences of invasions, and to stress that prompt and aggressive actions can reduce their impacts. I will highlight and contrast three *Phytophthora* species to make these points.

Indigenous and alien *Phytophthora* species

Phytophthora species are well-known in agriculture, limiting production of many crops from potatoes to citrus (Erwin and Ribeiro 1996). Classically, this is a genus of agricultural plant pathogens especially destructive in poorly drained soils or cool, wet climates (Table 1). The name derives from the Greek for "plant killer." These are Oomycetes, water molds, algal relatives, and not true fungi (Mycota) at all. Despite their unique phylogeny, they grow as filamentous hyphae and reproduce by spores, like fungi. They disperse and infect by motile zoospores, and survive unfavorable conditions, especially drying, as thick-walled chlamydospores or oospores. Most cause root diseases, but especially on trees, some cause lethal stem cankers, or infect foliage.

When forest trees are grown in agricultural settings, such as in nurseries, they are vulnerable to agricultural diseases, including Phytophthora root rots. The *Phytophthora* species commonly involved in forest nurseries are often the same species affecting agricultural commodities in the area. Douglas-fir seedlings, for example, are affected by *P. megasperma* and six other *Phytophthora* species when raised in poorly drained nursery soils (Hansen *et al*. 1979). Tree seedlings that are infected but survive in the nursery are likely to die in the first year after out planting onto forest sites. These nursery Phytophthoras, however, do not survive long in forest soils, and do not spread to surrounding trees (Roth and Kuhlman 1966, Hansen *et al*. 1980). They are adapted to agricultural soils and environments, and cannot compete in the more complex forest soil microbial community and generally drier, better drained forest soils. Other *Phytophthora* species do very well in forests, however.

In recent years, it has become clear that there is a very different community of *Phytophthora* species resident and probably indigenous in more or less undisturbed temperate forests. Many of these are new to science. For example, eight *Phytophthora* species were isolated from oak forest soils in the Forêt de Amance in NE France (Hansen and Delatour 1999). There were no obvious symptoms of Phytophthora root rot in this healthy mature stand, yet 12 of 14 soil samples from one site yielded one or more species. Five of the eight *Phytophthora* species were undescribed or only very recently described. Similar results have been obtained in Germany (Jung *et al*. 1996, 2002), eastern deciduous forests in the United States (Balci *et al*. 2007), and in the western US (author's unpubl. data). The indigenous forest *Phytophthora* community is numerous and diverse. In most cases, the Phytophthoras are confined to the fine roots of trees, and while they kill fine roots, under normal soil environmental conditions, the trees replace the roots without dramatic growth loss. In Europe *Phytophthora* species may contribute to the recurrent, chronic disease called oak decline. Oak decline, however, is primarily associated with periods of unusual drought, often coupled with outbreaks of defoliating insects. Under these stressful conditions, loss of additional rootlets to

Table 1. Some destructive *Phytophthora* species and the diseases they cause.

Pathogen	Disease	Host	Disease management
P. infestans	Late blight	Potato	Sanitation and Fungicides
P. sojae	Root and stem rot	Soybean	Resistant varieties
P. palmivora	Black pod	Cacao	Sanitation
P. alni	Collar rot	Alder	Clean nursery stock
P. cinnamomi	Jarrah dieback	Jarrah eucalyptus	Sanitation
	Littleleaf disease	Shortleaf pine	Change species
	Ink disease	Chestnut	Uncontrolled
	Avocado root rot	Avocado	Fungicides, soil management
P. lateralis	Cedar root disease	Port-Orford-cedar	Sanitation, avoidance, and resistance
P. ramorum	Sudden oak death, ramorum blight	Fagaceae, Ericaceae, and more	Quarantine and eradication

Phytophthora contributes to the decline (Hansen and Delatour 1999, Jung *et al*. 2000).

In contrast to the nursery soil Phytophthoras that are generally poorly adapted to forest soils, and to the indigenous *Phytophthora* community that persists in a dynamic equilibrium with its host trees, a few species qualify as truly destructive in forests. These are exotic, invasive species that can threaten the economic viability and ecological sustainability of the forests they attack. Distinguishing exotic from indigenous organisms can be more difficult than sometimes supposed, however.

An invading organism obviously originated someplace else; in the case of invasive Phytophthoras, the place of origin is generally unknown. Absent a documented evolutionary history, circumstantial evidence and presumption take on added weight. It is presumed that indigenous organisms do not cause dramatic disease in their native home, on their native hosts. The complex processes of coevolution will assure that host and pathogen coexist without either consistently impacting the reproductive fitness of the other. It is often presumed that the resulting disease symptoms will be subtle and perhaps difficult to detect, and the ecological impact will be slight. By this thinking, a *Phytophthora* species that kills trees rapidly and over an expanding area must be exotic.

This line of reasoning, while compelling in some situations, must be used with caution. *Phellinus weirii* is a pathogenic fungus that causes laminated root rot, a lethal disease of Douglas-fir in North American forests (Childs 1963). The disease is dramatic, altering forest structure and composition and pathways of succession (Hansen and Goheen 2000), yet the pathogen is indigenous to the forests where it is found.

Another presumed characteristic of an alien population is genetic uniformity. An invading population likely started as one or a few individuals making the first beachhead. This would be an evolutionary "bottleneck," and should result in reduced genetic diversity in the new population. Genetic diversity is readily measured in microorganism populations using a variety of molecular techniques. *Phytophthora* species, however, reproduce clonally as well as sexually, and many sexual species have in-breeding mating systems, rather than out-breeding. Therefore genetic diversity can be expected to be relatively low regardless of origin. But because there have been no studies of diversity in indigenous clonal or in-breeding species, there is no diversity baseline against which to compare a suspected invading population.

Three alien invaders

A number of *Phytophthora* species are invasive in various forests around the world today; three of them illustrate the range of impacts they can have, and the potentials for management response to limit ecological and economic damage. All are clearly alien to the forests they are presently altering so dramatically, but their epidemiology and their ecological impacts differ widely. Indeed, it is difficult to generalize on these matters. *Phytophthora lateralis* causes Port Orford Cedar Root Disease in western North America. *Phytophthora ramorum* is causing unprecedented mortality in oak and tanoak forests in California, as the cause of Sudden Oak Death, and *Phytophthora cinnamomi* kills trees in several parts of the world where it has been introduced, but nowhere more dramatically than in the Jarrah eucalyptus forests of western Australia.

Port-Orford-cedar (POC) or Lawson's cypress (*Chamaecyparis lawsoniana*) is endemic to mixed conifer forests in southwest Oregon and northwest California (Zobel *et al*. 1985). It is the principal known host for *Phytophthora lateralis,* the alien and invasive pathogen that has been killing POC since its introduction to the forest range of the tree near Coos Bay, Oregon, in about 1950. POC is a unique and valuable tree within its limited native range. It is a riparian species; only in the most fertile soils with relatively high rainfall, in the north, does it grow away from streams or other areas with a seasonally high water table. It usually grows in mixture with other conifers. It is one of a very few trees in the region that can tolerate ultramafic soils, however, and across thousands of hectares in the Klamath Mountains, it is the dominant tree.

POC is a long-lived tree, with decay resistant heartwood, and thick, fire resistant bark at maturity. It becomes increasingly important in late-successional forests. It regenerates abundantly in disturbed soil, however, and though slower growing than many of the early colonizing conifers like Douglas-fir, it is present in stands of all ages. The decay resistant, straight grained wood of mature and old-growth POC is very valuable, especially on the export market to Asian countries, where it substitutes for native Hinoki cypress, another *Chamaecyparis* species that is in short supply in its native Asian range. POC is also valued as a horticultural landscape tree. More than 100 variant individuals, differing in foliage color and growth form, have been selected in the wild, propagated, named, and entered the horticultural trade (Zobel *et al*. 1985).

The horticultural value of POC undoubtedly led to the introduction of *P. lateralis* to North America. The pathogen was first noted killing cedars in horticultural nurseries and landscape plantings about 1920. The disease (POC root disease) nearly eliminated POC from the nursery trade, but not before the pathogen was transported into the native forest range of the tree. Once in the forest, the economic value of the wood assured continued transport of the pathogen throughout the tree's range. It was carried in mud, on logging equipment, road maintenance vehicles, and passenger cars along the ever expanding road network. Vehicles took the pathogen uphill, and it washed downhill in the many streams of the region, killing nearly all cedars growing within root reach of water or roads (Hansen *et al*. 2000).

The swimming zoospores initiate infection of POC. Zoospores are attracted to young root tips, following gradients of root exudates in water saturated soils or where roots grow into streams. The pathogen colonizes the root system, killing the inner bark as it progresses (Oh and Hansen 2007). When it reaches the root collar the tree is girdled and becomes attractive to secondary bark beetles that are often the immediate cause of death. Meanwhile, the pathogen forms thick-walled, resistant chlamydospores in the dead roots which facilitate survival through seasonal dry periods. These resting spores are also transported on dirty equipment to new sites, where they may be activated in the next wet period and initiate new infections.

In the mountainous terrain where cedar grows, the pathogen moves uphill with human assistance, but is well adapted to downhill spread in flowing water. The resulting epidemic is closely tied to the forest road system, and to the streams that are infested as they cross those roads (Hansen *et al*. 2000, Betlejewski *et al*. 2003).

People first noticed coast live oak (*Quercus agrifolia*) and tanoak (*Lithocarpus densiflorus*) dying in alarming numbers about 1990, in woodlands and fragmented forests in suburban and rural residential areas near San Francisco, California. It wasn't until 2000, however, that the causal agent was discovered. Pathologists weren't looking for a *Phytophthora*, these trees were dying from infections on the main trunks — cankers that didn't originate from the roots. Yet *Phytophthora* it was. An undescribed species, soon to be named *P. ramorum*, was spreading from tree to tree above ground (Werres *et al*. 2001, Rizzo *et al*. 2002). Strangely, *P. ramorum*, the sudden oak death pathogen, is a close relative of *P. lateralis*, the cedar pathogen, with the same basic life cycle — swimming zoospores and thick-walled resting chlamydospores — but in this disease, the spores swim in films of water on leaf surfaces, and drip from the upper canopy of infected trees onto the main stems where they penetrate and kill the inner bark and sapwood.

Phytophthora ramorum spreads in three distinct ways: spores are splashed and drip downward in rain; spores produced on infected leaves are lofted into turbulent air and carried on air currents until they settle out by gravity or are washed out of the air by rain; and *P. ramorum* has been transported between states and continents on infected horticultural nursery plants (Rizzo *et al*. 2005). It is turbulent dispersal of airborne spores that allows *P. ramorum* to spread rapidly across the landscape. In Oregon, the spread has been mapped tree by tree and the dispersal gradient calculated.

Biannual or triannual SOD aerial detection surveys over the tanoak range in Oregon were conducted by Oregon Department of Forestry and the USDA Forest Service to locate recently dead tanoak trees. All trees mapped from the air were ground checked and cause of death determined. All *P. ramorum* identifications were con-

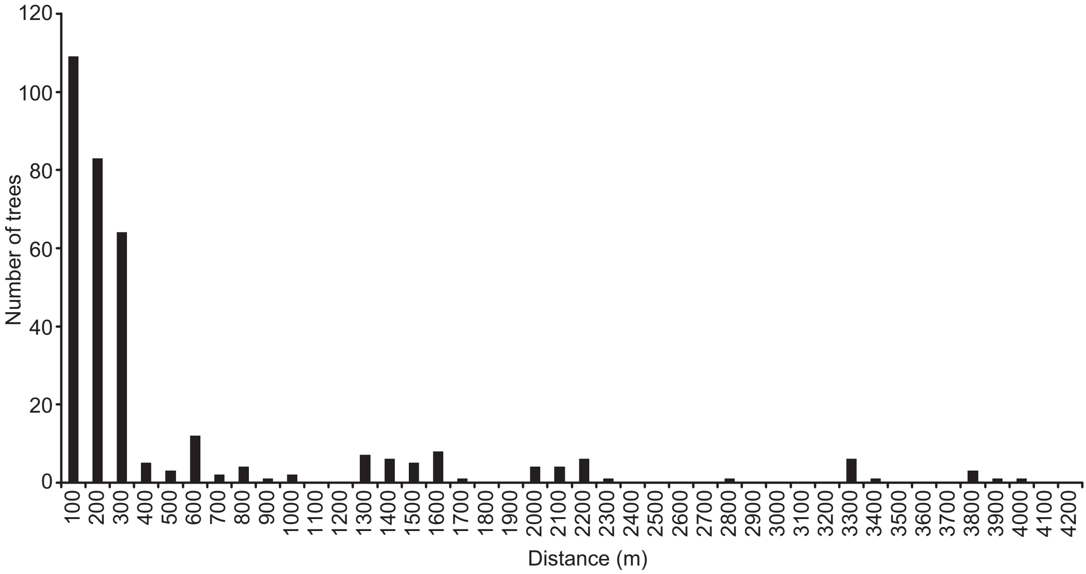

Fig. 1. Frequency distribution of apparent dispersal distances of *P. ramorum* in Oregon tanoak forests. Distances between tanoak trees killed by *P. ramorum* (2002–2006) and the nearest tanoak tree killed by the pathogen in a previous year were calculated and plotted by 100-m intervals.

firmed by direct isolation and/or diagnostic PCR. Tanoak trees testing positive for *P. ramorum* were geographically referenced with a hand-held global positioning system (GPS) instrument, and inter-tree distances were calculated. The apparent minimum dispersal distance between each tanoak tree confirmed to be infected by *P. ramorum* between 2002 and 2006 (n = 294) to the nearest tanoak with *P. ramorum* confirmed in any previous year was determined. Because of eradication, short distance dispersal was underrepresented. Most new infections occur within 300 m of previously infected trees, but rare events lead to jumps up to 4 km (Fig. 1). All of the trees more than 2750 m from a previously infected tree were detected in 2006.

Phytophthora ramorum also differs from *P. lateralis* in its host range. While *P. lateralis* is host specific, *P. ramorum* infects most of the plant species in western forests. Mortality is most dramatic in the oaks (sudden oak death), but rhododendrons and several other plants in the Ericaceae family are damaged (ramorum dieback). A miscellaneous array of plant species are susceptible to a lesser degree, usually suffering only scattered leaf spots (ramorum leaf blight) (Hansen *et al*. 2005).

Tanoak is the most susceptible species, but the myrtlewood tree, *Umbellularia californica*, harbors the pathogen without suffering serious damage itself, while supporting abundant production of spores which drive the epidemic in California (Davidson *et al*. 2005, Malony *et al*. 2005). It appears at this point that tanoak will be practically eliminated from northern and western portions of its range in California.

The economic value of tanoak over its entire range in Oregon and California is very low. On lands managed for timber production, it is considered a competitor with the much more desirable conifers. Dead, however, tanoak becomes a fire risk, in a region already averse to fire. The cost of tree removal to reduce fire risk is a financial burden to landowners. The tree produces acorns, and some animals and insects are dependent on this food source. The larger ecological importance of tanoak depends on the composition of the forest community where it is growing, and the successional stage of the stand.

Tanoak is an early successional species, colonizing quickly after stand replacing disturbance such as wildfire or timber harvest. It sprouts prolifically from stumps. Sudden oak death, however, kills the sprouts as well, eliminating the tree from infested sites. On many sites, tanoak is naturally overtopped by Douglas-fir and redwood in time, and becomes a less important part of the stand in late successional forests. In other areas there are extensive areas of nearly pure tanoak forest, usually following large wildfires, and loss of tanoak may force an extended period of chaparral vegetation. Tanoak also grows in mixture with other hardwoods, which in many situations will simply expand their crowns as the tanoak is killed, continuing the forest type, minus one species.

Phytophthora cinnamomi is the third of our infamous three, with the longest record of ecological destruction. Today it is killing a wide range of woody plants in warm temperate forests and wildlands in Australia, southern Africa, North America, and Europe (Erwin and Ribeiro 1996). Its origins are still unknown, although speculation centers on the islands of southeast Asia and the Pacific (Zentmeyer 1988). It was apparently first carried around the world on sailing ships, in roots and soil of exotic plants gathered by collectors for the estates and public gardens of the New and Old Worlds. It is soil borne like *P. lateralis*, but with a very broad host range. It destroyed the southern chestnut forest in the USA before chestnut blight, another alien invader arriving from the north, finished the job. One hundred years later, it resurfaced in the SE US as cause of littleleaf disease, a debilitating decline of shortleaf pine. In southern Europe today, *P. cinnamomi* is causing widespread decline of cork oak woodlands and in Australia it is considered one of the five most destructive environmental threats facing that continent. While it kills some species of eucalyptus trees and other plants in scattered areas of temperate forest throughout Australia, it is most destructive in Western Australia where it threatens the Jarrah eucalyptus (Banksia forest and woodlands), as well as the expansive heathlands with their rich flora of rare Gondwanaland endemics (Newhook and Podger 1972, Weste 1994).

The introduction of *P. cinnamomi* to Australia is lost in time. It was already widespread, and local damage was extensive before it was identified as the cause of "jarrah dieback" in 1964. It was another eight years before it was accepted that this was an exotic pathogen, not a native species gone "wild" in a disturbed environment (Newhook and Podger 1972). The epidemic was and is closely associated with humans and their activities in the bush, especially mining exploration, forest harvest, and recreation. New mortality centers are frequently associated with roads and trails. The aftermath is regularly a dramatically altered, and usually degraded, plant community. In the jarrah, for example, the *Banksia* species are especially susceptible and die first. The increase in inoculum from *Banksia* infection overcomes the jarrah. The iconic *Xanthoria*, the grass tree in the Lily family, is killed, as are most of the other shrub species and many herbs. The residual community is often dominated by grasses and sedges.

"Fight them on the beaches, or let the new order begin!"

Professor Hal Mooney of Stanford University was referring to alien, invasive plants when he delivered this rallying cry, but he is a vocal leader of the scientific community across the invasives spectrum. The "new order" refers to changed, often degraded ecosystems that often result from biological invasions. Disease control aimed at invasive forest pathogens is much of what forest pathologists do these days. Phytophthora diseases are important targets of these efforts to protect the ecological and economic values of forests at risk.

The Port-Orford-cedar root disease control program coordinated in federal forests in Oregon and Washington by the USDA Forest Service is integrated into all forest land management activities on National Forests in areas where cedar grows (Betlejewski 2003). The goals are straightforward. The plan strives to maintain the ecological and economic value of POC in its native range, by protecting the remaining uninfested areas, and restoring cedar in stands already devastated by *P. lateralis*. The strategy has three parts: (1) stop the spread of the pathogen into areas of healthy forest; (2) reduce inoculum levels in areas already damaged to slow disease intensification; and (3) restore the forest, bringing cedar back as an important part of degraded ecosystems. Tactics are varied and

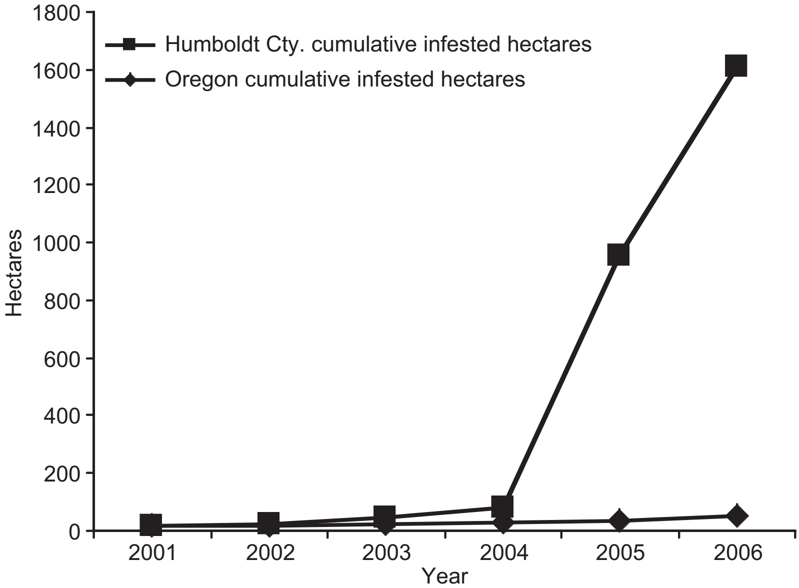

Fig. 2. Increase in tanoak forest area affected by *P. ramorum* from 2001–2006, in Humboldt Co. CA, without an eradication program and Curry Co. Oregon, with attempted eradication.

applied on a site specific basis after a risk analysis. They include seasonal and permanent road closures and washing vehicles before entering healthy forests, killing small POC where they have established in disturbed roadside soil, in order to reduce the opportunity for disease increase in the vulnerable roadside environment, and silvicultural actions to favor cedar in upslope topographic locations unlikely to be infested. A very successful feature of the POC management strategy is a range-wide program to screen for resistance to the pathogen in the surviving POC population, and to outplant disease resistant POC seedlings (Oh *et al*. 2006). Candidate individuals are tested for resistance by artificial inoculation and the winners are incorporated into containerized seed orchards. The program has progressed well, identifying several hundred parent trees with useful levels of resistance, and locally adapted resistant cedars are now available to public and private land managers.

Management actions against sudden oak death follow the same tripartite strategy of stopping spread, reducing inoculum, and restoring degraded forests (Rizzo *et al*. 2005). Because SOD still qualifies as a “new” disease, however, and because the forests at risk occur around the world, different parts of the program are emphasized in different regions. There is a major national and international quarantine and certified plant inspection program evolving to cut off pathways of spread through the nursery trade to uninfested areas.

In Oregon, at the northern limit of *P. ramorum* spread in the United States, eradication of new spot infections is being vigorously pursued. Intensive survey and monitoring, including regular aerial reconnaissance, is used to detect early infections, and trees in the near vicinity are cut and burned, hopefully before inoculum is produced and spreads further. The Oregon eradication program has not eliminated the pathogen from the state, but it has had a demonstrable effect on slowing the epidemic. The pathogen was introduced to Humboldt County in California at about the same time it was first detected in Oregon but it was not possible to sustain a control program there. After a lag phase of several years, the epidemic began to increase exponentially in Humboldt Co. In Oregon through 2006, the affected area continues to increase much more slowly (Fig. 2).

Further south in California, where the disease is already established, the situation is more discouraging. A slow the spread strategy is being tested, based on inoculum reduction targeting the understory hosts that support most of the production of sporangia, especially myrtlewood. Most effort, however, is going into managing the aftermath of the epidemic, especially through fuels reduction, and restoring forest cover by planting disease tolerant species. Programs to identify resistant oaks and tanoak, if they exist, are also beginning.

Some of the most dramatic and effective programs to manage an invasive forest pathogen are ongoing in Western Australia, directed against *Phytophthora cinnamomi*. One important tool is the *Phytophthora* specific fungicide phosphonate. At appropriate dosages, this compound stimulates host resistance to the pathogen, and decomposes to essentially phosphorous fertilizer. Phosphonate injected into the trunks of susceptible trees, especially *Banksia* species, provides four or five years of protection against subsequent infection by the pathogen (Shearer *et al*. 2006). Regular programs of injection are organized by volunteers in many areas to protect trees in parks and local natural areas.

Phosphonate is also applied from airplanes to protect susceptible vegetation in National Parks and other wildlands in the southwestern part of the state. The treatment program covers thousands of hectares annually. Without treatment, *P. cinnamomi* moves through susceptible plant communities at about 1 m a year, killing many of the rare endemic species as it passes. Phosphonate application reduces spread to nearly zero.

ALCOA Aluminum Company has institutionalized a voluntary, integrated "dieback management plan" on their lease holdings in Western Australia. ALCOA strip mines the lateritic soils for bauxite ore, then restores the land to its native vegetation. It is their publicly stated goal to leave the land with no more *P. cinnamomi* than was present when they took up the lease. The challenge is enormous given the scale of their operation and the nature of site disruption inherent in this kind of mining activity. They have been largely successful thru a program that starts with careful mapping of disease distribution and marking infested areas on the ground before any activity takes place. Equipment never passes from infested areas into clean areas without washing. Overburden from infested areas is stored separately from clean soil, and only returned to mined-out sites that were previously infested. Training of personnel is continuous, and dieback sanitation regulations are monitored and enforced by the company. Finally, results are regularly monitored, and corrections implemented as needed (Colquhoun and Hardy 2000).

Conclusions

Despite the close relationship between these three *Phytophthora* pathogens, and the essential similarity in life cycles, it is difficult to draw general principles about their ecological impacts on forest ecosystems beyond the fact that in each case they are contributing to the relentless homogenization and simplification of world ecosystems. Clearly breadth of host range of the pathogen makes a difference in ecological impact, but so do ecological features of the vulnerable hosts, whether they are early or late successional trees, for example, or grow naturally in pure stands or mixtures.

Although it is early days, it seems increasingly unlikely that these invasives will push any of their major susceptible hosts to final rangewide extinction. Local endemic plant species may not fair so well, but in general, the ecological amplitude of the trees seems to be greater than the *Phytophthora* species. Evolution and community dynamics still work. Death of one tree creates opportunities for other plants and the unexpected presence of rare resistance genes in cedar and jarrah creates opportunity, especially with human intervention, for selection and breeding for new, disease tolerant populations.

It is also clear that timely and aggressive disease management actions can at least slow the spread of these new diseases. Finally, it should be evident that the most cost effective solution to the problems created by invasive species is to prevent their establishment in the first place. Regional and international regulatory programs to restrict the predictable pathways by which pathogens move, many involving international trade, are the best hope for ecological sustainability of our natural ecosystems.

References

Balci Y., Balci S., Eggers J., Juzwik J., Long R., MacDonald W. & Gottschalk K. 2007. *Phytophthora* species associated with forest soils in eastern and north central U.S.

oak ecosystems. *Plant Disease* 91: 705–710.

Betlejewski F., Casavan K.C., Dawson A., Goheen D.J., Mastrofini K., Rose D.L. & White D.E. 2003. *A range-wide assessment of Port-Orford-cedar (Chamaecyparis lawsoniana) on federal lands*. USDA Forest Service Portland OR and USDI Bureau of Land Management, Salem OR, BLM/OR/WA/PL-004/004-1792.

Childs T.W. 1963. *Poria weirii* root rot. *Phytopathology* 53: 1124–1127.

Colquhoun I.J. & Hardy G.E.St.J. 2000. Managing the risks of Phytophthora root and collar rot during bauxite mining in the *Eucalyptus marginata* (Jarrah) forests of Western Australia. *Plant Disease* 84: 116–127.

Davidson J.M., Wickland A.C., Patterson H., Falk K. & Rizzo D.M. 2005. Transmission of *Phytophthora ramorum* in mixed-evergreen forests in California. *Phytopathology* 95: 587–596.

Erwin D. & Ribeiro O. 1996. *Phytophthora diseases worldwide*. APS Press, St. Paul, Minnesota.

Hansen E.M. & Delatour C. 1999. *Phytophthora* species in oak forests of north-east France. *Ann. For. Sci.* 56: 539–547.

Hansen E.M. & Goheen E. 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in western North America. *Ann. Rev. Phytopath.* 38: 515–539.

Hansen E.M., Parke J.L. & Sutton W. 2005. Susceptibility of Oregon forest trees and shrubs to *Phytophthora ramorum*: a comparison of artificial inoculation and natural infection. *Plant Disease* 89: 63–70.

Hansen E.M., Goheen D.J., Jules E. & Ullian B. 2000. Managing Port-Orford-cedar and the introduced pathogen *Phytophthora lateralis*. *Plant Disease* 84: 4–14.

Hansen E.M., Hamm P.B., Julis A.J. & Roth L.F. 1979. Isolation, incidence, and management of *Phytophthora* in forest tree nurseries in the Pacific Northwest. *Plant Disease Reporter* 63: 607–611.

Hansen E.M., Roth L.F., Hamm P.B. & Julis A.J. 1980. Survival, spread, and pathogenicity of *Phytophthora* spp. on Douglas-fir seedlings planted on forest sites. *Phytopathology* 70: 422–425.

Jung T., Blaschke H. & Neumann P. 1996. Isolation, identification and pathogenicity of *Phytophthora* species from declining oak stands. *European J. Forest Pathology* 26: 253–272.

Jung T., Blaschke H. & Osswald W. 2000. Involvement of *Phytophthora* species in central European oak decline and the effect of site factors on the disease. *Plant Pathology* 49: 706–718.

Jung T., Hansen E.M., Winton L., Osswald W. & Delatour C. 2002. Three new species of *Phytophthora* from European oak forests. *Mycological Research*. 106: 397–411.

Malony P.E., Lynch S.C., Kane S.F., Jensen C.E. & Rizzo D.M. 2005. Establishment of an emerging generalist pathogen in redwood forest communities. *J. Ecol.* 93: 899–905.

Newhook F.J. & Podger F.D. 1972. The role of *Phytophthora cinnamomi* in Australian and New Zealand forests. *Annu. Rev. Phytopathol.* 10: 299–326.

Oh E. & Hansen E.M. 2007. Histopathology of infection and colonization of Port-Orford-cedar by *Phytophthora lateralis*. *Phytopathology* 97: 684–693.

Oh E., Hansen E.M. & Sniezko R.A. 2006. Port-Orford-cedar resistant to *Phytophthora lateralis*. *Forest Pathology* 36: 385–394.

Rizzo D.M., Garbelotto M. & Hansen E.M. 2005. *Phytophthora ramorum*: Integrative research and management of an emerging pathogen in California and Oregon forests. *Annu. Rev. Phytopathol.* 43: 309–345.

Rizzo D.M., Garbelotto M., Davidson J.M. & Slaughter G.W. 2002. *Phytophthora ramorum* as the cause of extensive mortality of *Quercus* spp. and *Lithocarpus densiflorus* in California. *Plant Disease* 86: 205–214.

Roth L.F. & Kuhlman E.G. 1966. *Phytophthora cinnamomi*, an unlikely threat to Douglas-fir forestry. *Forest Science* 12: 147–159.

Shearer B.L., Fairman R.G. & Grant M.J. 2006. Effective concentration of phosphite in controlling *Phytophthora cinnamomi* following stem injection of *Banksia* species and *Eucalyptus marginata*. *Forest Pathology* 36: 119–135.

Werres S., Marwitz R., Man In't Veld W.A., De Cock A.W.A.M., Bonants P.J.M., De Weerdt M., Themann K., Ilieva E. & Baayen R.P. 2001. *Phytophthora ramorum* sp. nov., a new pathogen on *Rhododendron* and *Viburnum*. *Mycological Research* 105: 1155–1165.

Weste G. 1994. Impact of *Phytophthora* species on native vegetation of Australia and Papua New Guinea. *Australasian Plant Pathology* 23: 190–209.

Zentmeyer G.A. 1988. Origin and distribution of four species of *Phytophthora*. *Trans. Brit. Mycol. Soc.* 91: 367–379.

Zobel D.B., Roth L.F. & Hawk G.M. 1985: *Ecology, pathology, and management of Port-Orford-cedar (Chamaecyparis lawsoniana)*. U.S.D.A. Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-184.