Phytophthora root disease and the need for clean nursery stock in urban forests: Part 1

Phytophthora invasions in the urban forest and beyond

Tedmund J. Swiecki, Elizabeth A. Bernhardt, and Susan J. Frankel

ROOT ROTS AND OTHER diseases caused by *Phytophthora* species have long been recognized as serious problems in agriculture, nurseries, various landscape plants, and some forests (Erwin and Ribeiro 1995). Even though most arborists and urban foresters are aware of these pathogens, the effects that root-infecting *Phytophthora* species have on the health and sustainability of urban forests are not well understood. Recent research suggests that introduced *Phytophthora* species pose an increasingly important threat to both urban forests and their surrounding native forests and plant communities (Barber et al. 2013, Beckerman et al. 2014, Brasier 2008, Dale et al. 2017, Hulbert et al. 2017, Jung et al. 2015, Scanu et al. 2015, Swiecki et al. 2011). In this series of articles, we will discuss root rots caused by *Phytophthora* in both urban forests and wildlands, with emphasis on information from California.

When introduced into native ecosystems, various exotic *Phytophthora* species have proven to be serious pathogens (Hansen et al. 2000, Henricot et al. 2017, James 2011a,b; Jung et al. 2018, Jung and Blaschke 2004, Rizzo et al. 2002, Swiecki et al. 2011, Wills 1993). Sudden oak death, caused by *Phytophthora ramorum* (Rizzo et al. 2002), Port-Orford-cedar root disease, caused by *P. lateralis* (Betlejewski et al. 2011), and root rot caused by *P. cinnamomi* (Swiecki et al. 2011) are notable examples of Phytophthora diseases that are severely affecting native forests and other native plant communities in California (**Figs. 1-2**).

Phytophthora biology

Phytophthora species are microscopic plant pathogens in the Oomycota, a group also known as the water molds. Water molds were formerly classified with the fungi but are now known to be more closely related to the brown algae in a taxonomic group known as the stramenopiles. More than 160 species of *Phytophthora* have been described, but new, undescribed species are still being isolated from affected plants and habitats. Most of these *Phytophthora* species are pathogens that can severely damage or kill susceptible hosts, which include a wide variety of agricultural, ornamental, and native plants. Diseases caused by *Phytophthora* species include root roots, stem and trunk cankers (**Fig. 3**), and blights of fruit and leaves. Host ranges of individual *Phytophthora* species vary. Some species can infect hundreds to thousands of plant species across many plant families, whereas others have relatively limited host ranges.

Figure 1. *Phytophthora cinnamomi* root disease center in Ione manzanita (*Arctostaphylos myrtifolia*) habitat in Amador County. Long-dead plants are gray and defoliated. Small dead plants with brown leaves (foreground) are recently killed seedlings of whiteleaf manzanita (*A. viscida*). Manzanita seedlings that germinate in old root disease centers typically may survive for a few years until they are infected and killed by *P. cinnamomi* that persists in the soil. Trees in background (foothill pine, *Pinus sabiniana* and interior live oak, *Quercus wislizeni*) are much less sensitive to this pathogen.

Figure 2. *Phytophthora cinnamomi* causes decline and mortality of many California natives, including these Pacific madrone (left) (*Arbutus menziesii*) and California bay (right) (*Umbellularia californica*) trees in China Camp State Park (Marin County).

Introduced Phytophthora species pose an increasingly important threat to both urban forests and their surrounding native forests and plant communities pathogens.

Effects of root-rotting *Phytophthora* species are generally underrecognized because the symptoms they produce on above-ground portions of trees and other woody plants are not unique. The most common symptoms of Phytophthora root rot are reduced growth, water stress-related symptoms, and decline (**Figs. 2, 4, 5**). Especially in urban landscapes, these symptoms are commonly attributed to cultural factors, such as inadequate or excessive irrigation. Sometimes, more obvious secondary agents (such as wood-boring beetles or fungal stem cankers) that invade severely stressed or declining trees may be misidentified as the primary agent of decline. Without specific testing for soil *Phytophthora* species in such situations, the involvement of these pathogens is typically not recognized. Because *Phytophthora* species can persist in soils after affected plants have been removed, they have the potential to affect replantings and pose an ongoing but unrecognized threat to urban forest health.

Phytophthora disease cycle

The Phytophthora root rot disease cycle (**Fig. 6**) is strongly influenced by the presence of water. Disease cycling (**Fig. 6, upper half**) occurs under moist conditions that include at least brief periods of free water. Free water is present in soils that are flooded or saturated, as well as in water-filled pores in partially-drained soils wetted by rain or irrigation. Free water promotes the release of motile, root-

Figure 3. This *Quercus robur* in a Solano County yard shows extensive bleeding trunk cankers caused by *Phytophthora cinnamomi*. Bleeding trunk cankers sometimes develop in association Phytophthora root rots, more commonly in irrigated areas than in dry sites.

Figure 4. Decline and dieback of young valley oak (left) (*Quercus lobata*) and coast live oak (right) (*Q. agrifolia)* trees associated with *Phytophthora cambivora* infestations in San Mateo County.

infecting zoospores from sporangia. Although long periods of soil saturation promote *Phytophthora* reproduction, relatively short periods that are typically associated with rain or irrigation events are sufficient for zoospore release to occur. *Phytophthora* sporangia can develop and persist under a wider range of soil moisture levels. Some species produce sporangia more readily in moist soil than in saturated soil (MacDonald and Duniway 1978).

Figure 5. This dying nursery-grown coast live oak in a restoration planting in the Angeles National Forest (Los Angeles County) was infected with *Phytophthora cactorum* and *P. niederhauserii*.

The disease cycle for Phytophthora root rot (**Fig. 6**) can be completed rapidly. Sporangia capable of producing zoospores can be formed in as little as 24 hours after a susceptible root is infected by zoospores (Swiecki and MacDonald 1998). Hundreds of sporangia can develop on a short section of infected root and each sporangium can release 20 to 50 zoospores. Consequently, inoculum levels can increase explosively under favorable conditions, leading to rapid disease development and spread.

Phytophthora species are well-adapted to survive under suboptimal conditions. When conditions are too dry for sporangium production, *Phytophthora* hyphae can produce resistant survival structures (**Fig. 6, lower right**). These structures can tolerate drying and persist in dead root fragments or soil. *Phytophthora*-infested soil and plant debris can be inadvertently transported on tools, vehicles, and shoes, or moved in large quantities when infested soil is excavated, graded, or imported. In the presence of appropriate stimuli, such as moisture and root exudates, resistant structures germinate to produce sporangia or hyphae, leading to new infections. *Phytophthora* sporangia of some species can also survive considerable drying and release zoospores when rewetted (MacDonald and Duniway 1978).

Phytophthora in and near urban environments

Phytophthora root rots are discussed in many urban forest pest and disease reference publications. However, few studies have examined how these diseases affect urban forest health. Barber et al. (2013) used baiting and direct isolation to recover *Phytophthora* species from urban streetscapes, parks, gardens, and remnant native vegetation in urban settings in Perth and the southwest portion of Western Australia. They found a wide variety of *Phytophthora* species associated with decline and mortality of these urban trees. *Phy-*

tophthora species were recovered from 69 of 230 sampled sites (30%). This percentage likely underestimates the actual rate of infestation because false negatives are common in such samples. Nine species of *Phytophthora* were found in association with a wide variety of host species. The *Phytophthora* detections included three previously undescribed species, another species not previously found in Australia, and additional species found in nurseries or other settings but not previously known from urban trees. Furthermore, the most commonly detected species, *P. multivora*, has also been associated with the decline and mortality of many native species in natural ecosystems across Western Australia (Barber et al. 2013).

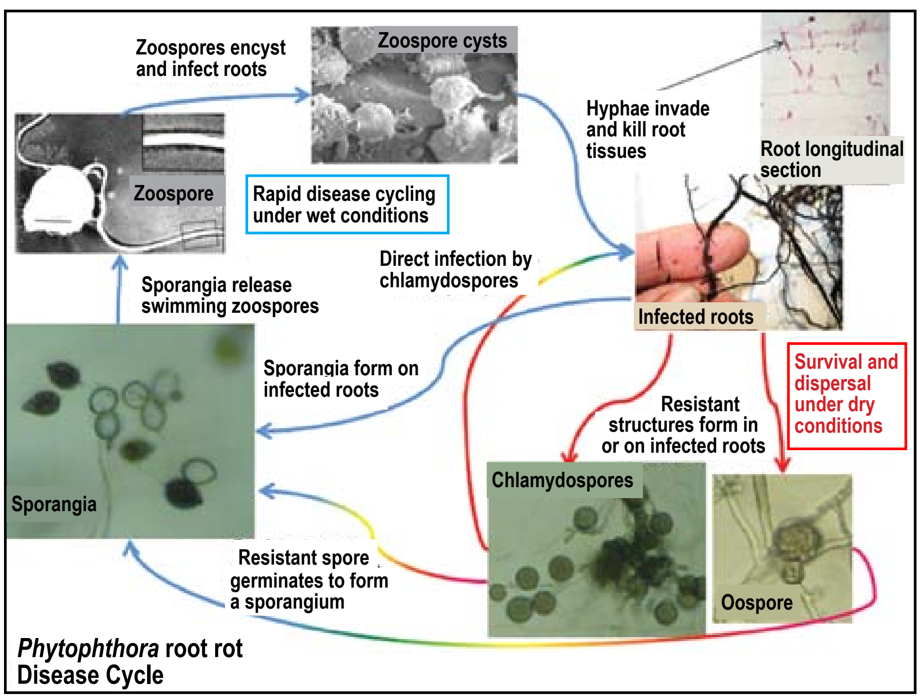
Jung et al. (2015) presented data gathered over many years from European nurseries and planted sites in urban landscapes and forests. They documented hundreds of previously unknown host-pathogen associations in both nurseries and plantings. They found 56 *Phytophthora* taxa in 2525 forest and landscape planting sites, including five undescribed *Phytophthora* taxa. *Phytophthora* infestations were detected in 66% of the planting sites. Symptoms in affected plants included fine root loss, stem cankers, crown decline, wilting, and plant mortality. The authors concluded that diseases caused by *Phytophthora* pose a substantial threat to both planted landscapes and forest ecosystems and that widespread contamination of nursery stock was the primary means by which these pathogens were introduced and spread in Europe.

More recently Dale et al. (2017) used baiting and DNA metabarcoding to identify *Phytophthora* species in soil and water from environments that were categorized as urban, natural, or urban/natural interface in British Columbia. *Phytophthora* species were detected much more frequently in soil samples from urban and interface sites than in natural sites. More than twice as many *Phytophthora* species were detected in urban samples (23) than in natural samples (11). Urban samples also showed a much higher diversity of *Phytophthora* per sampling site than natural environments. Furthermore, most of the uncommon species, which included six undescribed species, were only found in urban or interface areas. This suggests that these *Phytophthora* species had been introduced initially into urban areas and had subsequently spread into native vegetation, particularly in interface areas.

Because Phytophthora root rots are known to be common in urban forest species, they are commonly overlooked unless associated with unusual mortality or decline of significant trees. For example, in 2006, widespread mortality within an urban planting of Italian alder (*Alnus cordata*) in a northern California city was shown to be due to *P. siskiyouensis* (Rooney-Latham et al. 2009). We found *Phytophthora cactorum* associated with recent Catalina ironwood (*Lyonothamnus floribundus* ssp. *asplenifolius*) street tree plantings in San Francisco that were dying at high rates. We have also found that this tree can be infected by *P. hedraiandra* and *P. niederhauserii*. The SelecTree database (**https://selectree.calpoly.edu**) entry for this species notes "needs good drainage". For this species and probably many others, such cultural notes are partly or entirely related to susceptibility to Phytophthora root rots.

As noted by Jung et al. (2015), multiple *Phytophthora* species are commonly present in a single urban forest site. In sampling we have conducted in northern and southern California sites where nursery stock had been planted, we have repeatedly found multiple *Phytophthora* species within a given site. The presence of multiple *Phytophthora* species increases the potential for damage because the host ranges of these pathogens vary. Plants that may

Figure 6. General disease cycle for root-rotting *Phytophthora* species. Upper loop (solid blue arrows) illustrates rapid disease cycling that occurs under generally moist conditions, with at least intermittent soil saturation. Cycling that enables pathogen survival and dispersal under drier conditions is shown with red and multicolored arrows.



have some resistance to one *Phytophthora* may be killed by a second *Phytophthora* at the sites.

We have identified multiple locations in northern California where introduced *Phytophthora* species, especially *P. cinnamomi* and *P. cambivora*, have caused localized to extensive decline and mortality in native forests and shrublands (Swiecki et al. 2011). These include habitat of Ione manzanita (*Arctostaphylos myrtifolia*) in the dry foothills of the Sierra Nevada in Amador County (**Fig. 1**), the very limited habitat of pallid manzanita (*A. pallida*) adjoining urban development in the Oakland Hills (Alameda and Contra Costa Counties), and multiple woodlands with declining native trees including oaks (*Quercus agrifolia*, *Q. douglasii*, *Q. lobata*) (**Fig. 4**), madrone (*Arbutus menziesii*) (**Fig. 2**), California bay (**Fig. 2**), and giant chinquapin (*Chrysolepis chrysophylla*). A key point is that virtually all these *Phytophthora* infestations have developed in dry sites not subject to flooding or irrigation. Winter-spring rainfall is adequate to sustain Phytophthora root rot in susceptible species in California.

Another important point is that no *Phytophthora* species has yet been demonstrated to be native to California. Most of the most common species detected in California are distributed globally, having been moved about with live plants or other infested materials. As has been documented for *P. ramorum*, introduced *Phytophthora* species can become widely-distributed and firmly-established in invaded landscapes before they are detected for the first time. *P. siskiyouensis*, noted above, was thought to be native to forested areas of southwestern Oregon, where it was initially detected during monitoring of streams and soil for *Phytophthora ramorum* (Reeser et al. 2007). However, Reeser et al. (2007) were unaware that this species was already circulating in the nursery industry and had been previously detected on dying urban alders (*A. glutinosa*) in Australia (Smith et al. 2006).

Phytophthora persistence

Infestations of soil-borne *Phytophthora* species are persistent and very difficult to eliminate. Many species have wide host ranges. Some infected hosts may survive for many years, continuing to produce inoculum that can be spread to other areas. Most root-rotting *Phytophthora* species also produce resistant spores that can survive for years in the absence of a living host. Long-term persistence of *P. cinnamomi* has been documented in Australian forests in the absence of known primary hosts. At least some of this persistence may be due to unrecognized and asymptomatic infections in previously unknown hosts, including various annuals and herbaceous perennials (Crone et al. 2013).

Residual *P. cinnamomi* inoculum can prevent recolonization of old mortality centers in affected stands of Ione manzanita (Swiecki and Bernhardt 2003, 2016). Although seed of susceptible manzanitas (*A. myrtifolia* and *A. viscida*) will eventually sprout in areas where the stand had been killed many years earlier, seedlings become infected and killed within a few years (**Fig. 1**). In one northern California street planting of cork oaks (*Quercus suber*), we identified mortality due Phytophthora root rot in 1994; tree decline and mortality were still occurring 21 years later. Both *P. cinnamomi* and *P. cactorum* were recovered from roots and soil beneath affected trees in 2015. Another example of long-term *Phytophthora* persistence was demonstrated in an undeveloped urban site in the San Francisco Bay Area. This vacant parcel had a mix of old trees and woody shrubs of various exotic species, a few of which had died recently. In 2015, we sampled around existing and recently-removed woody vegetation at the site and recovered *P. cinnamomi* and *P. cryptogea* by baiting from multiple sample locations. The presence of these pathogens appeared to be related to the previous use of the site: a municipal woody plant nursery and adjacent residence that was in use for at least several decades in the first half of the twentieth century. The structures had been removed and the site was unoccupied and unmanaged for at least 60 years before sampling.

Spread of *Phytophthora*

Phytophthora root disease centers expand over time as infections spread from root to root in the soil. Spread can occur through root-to-root contact or infections initiated by zoospores released from sporangia on nearby infected roots. Activities that move infested debris, soil, or water along roads and trails can also contribute to spread. Such patterns of spread have been observed in connection with *P. cinnamomi* in Australia (Colquhoun and Hardy 2000) and P. lateralis in California (Hansen et al. 2000). Livestock are also implicated in *Phytophthora* transport in some locations, where they can track mud between water sources.

Zoospores, which swim upward (due to negative geotaxis), can also reach the soil surface under flooded conditions and be moved great distances with flowing water. Some *Phytophthora* species (especially members of *Phytophthora* clade 6) persist in watercourses, and others that are normally found in the soil can be washed downhill with flowing water or into creeks and rivers with storm runoff.

In a study of relatively undeveloped parks and preserves in Santa Clara County (Swiecki and Bernhardt 2018), we detected *Phytophthora* species in 67% of 21 water samples collected across multiple locations. We have also detected *Phytophthora* in ponds, creeks, and ponded or flowing storm runoff in many other northern California locations. Flowing water, including seasonal runoff, has been implicated in *Phytophthora* spread in many locations. In the Santa Clara study, *Phytophthora* species were recovered more frequently in samples of natural vegetation from periodically flooded sites (59%) than from drier upland and flat/lowland sites (9%).

In the Santa Clara County study (Swiecki and Bernhardt 2018), most terrestrial *Phytophthora* detections were found in sites where contamination was likely to have come from other infested areas, most commonly urban landscaping or habitat restoration sites planted with nursery stock. Another apparent *Phytophthora* source was historical orchard lands, which were very extensive in Santa Clara Valley until they were replaced by urban development in the second half of the 20th century. From infested areas, *Phytophthora* has apparently spread into native habitats by various routes, including watercourses, roads, and trails.

Phytophthora in California habitat restoration plantings

Recent research in habitat restoration plantings have highlighted the scope of the *Phytophthora* problem in California. In 2014, *P. tentaculata* was detected in planted nursery stock at two large habitat restoration sites in northern California (Rooney-Latham et al. 2015). This pathogen had only been found once before in the US, at a California native plant nursery different from the supplier of the contaminated stock identified in 2014. In subsequent sampling (Bourret et al. 2016, Rooney-Latham et al. 2016), about 60 different *Phytophthora* taxa were identified in restoration planting sites and native plant nurseries. The sampled restoration plantings were mostly located in urban riparian corridors and peri-urban parks, open spaces, or protected watersheds.

At one northern California site, a large (about 7 acres) area of native vegetation showing decline and mortality of multiple plant species was found to be infested with multiple *Phytophthora* species, including *P. cactorum, P. cambivora, P. crassamura, P. 'kelmania'* and *P. syringae*. Several groups of *Ceanothus* nursery stock that were planted at the site 22 years earlier as part of a habitat restoration project were the apparent source of the infestation across this sloped site. Subsequent spread was primarily downhill from the planting sites, facilitated by water flow, with additional spread along and near trails (Swiecki and Bernhardt 2018).

In these California studies, *Phytophthora* species were detected by baiting, isolation, or in some cases, by direct detection of DNA in root tissue. *Phytophthora* species were found in nursery stock that included a wide variety of trees, woody and semi-woody shrubs, and some sedges and rushes. Most of the specific host-*Phytophthora* interactions identified were previously unknown. In most situations, sampled plants were declining, recently dead, or stunted, but some plants did not show obvious symptoms. *Phytophthora* species were also recovered from planting sites where the plant was long dead or no longer present. In multiple cases, two or more *Phytophthora* species were recovered from a single outplanted nursery plant. *Phytophthora* detections have included at least five previously undescribed species and the first known detection in the US of *P. quercina* (Bourret et al. 2016). Both *P. quercina* (ranked 1) and *P. tentaculata* (ranked 5) were among the top five *Phytophthora* species not yet detected in the US that were identified as significant threats in a 2006 USDA Pest Risk analysis (Schwartzburg et al. 2009).

Phytophthora and nursery stock

A common thread connecting most of the situations described above is the involvement of nursery stock infested with *Phytophthora* species. Many *Phytophthora* species that cause root and crown rots are closely associated with urban landscapes because they are most commonly introduced via nursery stock (Baker 1957, Crandall et al. 1945, Ferguson and Jeffers 1999, Jung et al. 2015, Jung et al. 2018, MacDonald et al. 1994, Standish 1982, Zentmyer et al. 1952). Dissemination of *Phytophthora* species in nursery stock has been recognized for decades, and many studies have documented widespread *Phytophthora* infestation in nurseries. Thirteen species of *Phytophthora* were found in a survey for leaf spots in California nurseries in 2005 and 2006 (Yakabe et al. 2009). Eleven *Phytophthora* taxa were found in a survey of Minnesota nurseries for *Phytophthora* species causing symptoms primarily on aboveground plant parts (Schwingle et al. 2007). Two of the taxa were potential hybrids, one was apparently an undescribed species, and one (*P. hedraiandra*) had not previously been known in the US when it was detected in 2002. At least eight species of *Phytophthora* were found in arriving shipments of symptomatic and asymptomatic plants from west coast nurseries to Maryland (Bienapfl and Balci 2014). In a year-long, detailed study of four Oregon nurseries, Parke et al. (2014) identified 28 *Phytophthora* taxa, including several likely hybrids. Jung et al. (2015) reported 49 *Phytophthora* taxa found in 670 European nurseries. *Phytophthora* species were recovered from more than 90% of the sampled nurseries in that large study. As noted above, sampling of plants in or originating from California native plant nurseries alone has yielded about 60 *Phytophthora* taxa to date (Bourret et al. 2016, Rooney-Latham et al. 2016).

These and many other studies have shown that nursery stock is very commonly infested with multiple *Phytophthora* species that can infect a wide variety of plant species. Furthermore, international trade in nursery stock serves as a major conduit for the rapid dispersal of these pathogens globally (Brasier 2008, Liebhold et al. 2012, Santini et al. 2013). Beyond official trade, undocumented international movement of plant material occurs on a regular basis by individuals who are unaware of phytosanitary regulations or simply wish to bypass them. As a result, new species of *Phytophthora* continue to appear in the nursery trade, in some cases surfacing almost simultaneously in many countries, as was the case for *P. niederhauserii* (Abad et al. 2014).

Conclusions

Phytophthora root rots are proving to be a more varied and pervasive threat to both urban and native forests than many arborists and urban forestry professionals have realized. Far from being limited to overwatered landscapes, *Phytophthora* species also cause root rot and decline in dry habitats. In the presence of susceptible hosts, Phytophthora root rots can develop with only the moisture provided by rainfall.

It is also noteworthy that *Phytophthora* species are not found everywhere. Research in California shows that these pathogens are most likely to be found where they have been introduced and can infect susceptible vegetation. Unfortunately, one of the most common arboricultural practices, planting nursery stock, is one of the most common routes by which exotic *Phytophthora* species are introduced into the landscape. Hence, the large and increasingly diverse contingent of *Phytophthora* species identified in nursery stock present an expanding threat to urban and native forests alike. In the following installments, we will explore why *Phytophthora* is so common in nursery stock, how to avoid introducing *Phytophthora*, and how to manage existing infestations.

Tedmund J. Swiecki
Principal / Plant Pathologist
Phytosphere Research, Vacaville, California
phytosphere@phytosphere.com

Elizabeth A. Bernhardt
Principal / Plant Pathologist
Phytosphere Research, Vacaville, California

Susan J. Frankel
Plant Pathologist
USDA Forest Service, Pacific Southwest Research Station
Albany, California

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