Swiecki et al.: *Phytophthora cinnamomi* Threat
Proceedings of the CNPS Conservation Conference, 17–19 Jan 2009
pp. 367–371

THE EXOTIC PLANT PATHOGEN *PHYTOPHTHORA CINNAMOMI:* A MAJOR THREAT TO RARE *ARCTOSTAPHYLOS* AND MUCH MORE

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ABSTRACT

Phytophthora cinnamomi, introduced into California by the early 20th century, is a serious root pathogen of many agricultural and horticultural species in the state. We determined that *P. cinnamomi* causes a lethal root rot of the threatened *Arctostaphylos myrtifolia* and is the cause of extensive *A. myrtifolia* mortality throughout the northern half of this plant's limited range in Amador County. The persistence of *P. cinnamomi* in soils renders pathogen-infested habitats unable to support *A. myrtifolia*. Consequently, *A. myrtifolia* conservation depends on stopping further pathogen spread. We subsequently found *P. cinnamomi* killing the endangered *A. pallida* and other native woody species in protected native habitat in the Oakland Hills, as well as *Arbutus menziesii* and *Umbellularia californica* in native stands in Marin and Sonoma Counties. *Phytophthora cinnamomi* has been isolated from container stock purchased from several native plant nurseries, suggesting nursery stock used for restoration projects or planted in the wildland-urban interface can provide a route for native habitat invasion. These and other findings indicate that *P. cinnamomi* is a developing threat to California native flora. Phytosanitary measures must be considered to prevent further introduction and spread of *P. cinnamomi* in many California plant communities.

Key words: *Arctostaphylos myrtifolia*, native habitat, nursery, *Phytophthora cinnamomi*, plant disease, rare plants, sanitation.

INTRODUCTION

Phytophthora cinnamomi Rands is a serious soilborne pathogen of both agricultural crops and native plant communities in temperate, subtropical, and tropical regions and on all continents except Antarctica. *Phytophthora cinnamomi* is a fungus-like organism most closely related to diatoms and kelp (Kingdom Stramenopilia) rather than to the true fungi (Kingdom Fungi or Eumycota). It is an introduced exotic pathogen in North America. Its native range is unknown, but is suspected to be southeast Asia. Human-related activities, including the international plant trade have facilitated spread of *P. cinnamomi* into numerous habitats worldwide. *Phytophthora cinnamomi* causes lethal diseases in an unusually large number of plant species, including many woody dicots and conifers. It commonly causes root decay, but can also colonize and kill above-ground portions of some host plants. In western Australia alone, where *P. cinnamomi* has invaded and devastated several hundred thousand hectares of native forests, the host range is estimated to include over 2000 species (Wills 1993). This pathogen has brought a number of Australian rare plant species to the brink of extinction.

For the past 100 years, *P. cinnamomi* has been known in California as a pathogen of commercial fruit and nut orchards and ornamental plants, including nursery stock. Only recently has *P. cinnamomi* been documented killing California native plants in their native habitats (Swiecki et al. 2003; Garbelotto et al. 2006). *Phytophthora cinnamomi* is very persistent in soils and cannot be eradicated from native habitats that it invades. In many infested sites, disease management is limited to preventing further pathogen spread.

Here we discuss how *P. cinnamomi* has invaded the habitat of the rare and threatened *Arctostaphylos myrtifolia* Parry, leading to extensive losses of this plant and its limited habitat. This finding led us to identify other areas where *P. cinnamomi* is killing native plants in wildland settings. We identify pathways by which *P. cinnamomi* has entered wildlands, and discuss ways to limit the threat this pathogen poses to noninfested native ecosystems.

PHYTOPHTHORA CINNAMOMI AND *ARCTOSTAPHYLOS MYRTIFOLIA*

Arctostaphylos myrtifolia is limited to the unusual, highly acidic soils of the Ione formation in the central

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Sierra Nevada foothills. Large areas of mortality in stands of *A. myrtifolia* south of Ione, California, were noted as early as 1988 (Wood and Parker 1989), but the cause of this mortality remained unknown. In 2002, we determined that *P. cinnamomi* causes the root and crown rot that has killed large patches of *A. myrtifolia* and *A. viscida* Parry in Ione formation soils (Swiecki and Bernhardt 2003; Swiecki et al. 2003). This was the first report of *P. cinnamomi* causing extensive mortality in a California native plant community. Introduction of *P. cinnamomi* into this ecosystem constitutes a long-term and possibly permanent destruction of *A. myrtifolia* habitat.

CONDITIONS FAVORING DISEASE

Phytophthora cinnamomi survives in the soil in infected roots and as survival spores (chlamydospores) that can persist for many years in the absence of susceptible hosts. When soils are moist, chlamydospores can germinate and initiate new infections in nearby roots. In moist, unsaturated soil, *P. cinnamomi* sporangia are produced on infected roots. When soils become saturated by rainfall or flowing water, motile zoospores are released from sporangia. Zoospores swim to host roots, attracted by compounds exuded by the roots. Zoospores encyst on or near roots and germinate to produce filamentous hyphae that penetrate and proliferate within host roots, ultimately killing the roots. Multiple sporulation and infection cycles may occur as soil moisture fluctuates during the rainy season or under irrigated conditions (Zentmyer 1980).

In agricultural systems, *P. cinnamomi* is commonly associated with low, poorly drained areas. However, in *A. myrtifolia* habitat, severe disease is prevalent on slopes and hilltops in a region notable for the severity of its summer drought conditions. Nonetheless, during rainy periods lasting for a day or more, even well-drained soils on slopes can remain saturated long enough to allow for zoospore release and root infection. We experimentally induced lethal root rot in *A. myrtifolia* transplanted into naturally-infested field soil with regular irrigation and only a single 12 hr flooding period. Due to temperature limitations for sporulation and growth (Zentmyer 1980), most new infections in *A. myrtifolia* habitat are likely to be initiated during warm spring and/or fall rain events.

Spread of P. cinnamomi *within* A. myrtifolia *Habitat*

We conducted a survey of *A. myrtifolia* mortality centers in the Ione area to assess prevalence and study the genetics of *P. cinnamomi* (Swiecki et al. 2005). The pathogen was widespread throughout much of the northern portion of *A. myrtifolia's* range in Amador County. DNA microsatellite analyses showed that 5 different genetic variants were present among the *P. cinnamomi* isolates recovered from various mortality centers. The presence of these different variants indicates that *P. cinnamomi* has been introduced into *A. myrtifolia* habitat multiple times over the years.

One of the largest and oldest *A. myrtifolia* mortality centers is located along SR88 south of Ione, spanning an area approximately 2.5 km^2. All *P. cinnamomi* strains collected from this area were the same genetic variant, suggesting that mortality in this area is largely due to spread from a single pathogen introduction. This variant is widely dispersed in the Ione area. Near the northern limit of the *A. myrtifolia* range near Carbondale Road, mortality within a smaller, more recent infestation was also associated with a single—but different—genetic variant. This strain and a closely related variant were also found more than 15 km to the south in a mortality center south of SR88.

The greatest diversity of *P. cinnamomi* was found at a preserve established to protect rare plants unique to Ione formation soils, including *A. myrtifolia.* Multiple *P. cinnamomi* mortality centers and at least four genetically distinct pathogen variants were observed at the fenced Apricum Hill Preserve along Jackson Valley Road south of SR88. The diversity in the pathogen population suggests multiple pathogen introductions from at least four separate sources. *Phytophthora cinnamomi* can be transmitted via contaminated shoes and tools. The various introductions of the pathogen at Apricum Hill are likely due to the preserve's visitors, primarily researchers, agency personnel, and students. Supporting this hypothesis, most mortality centers are relatively small, suggesting that their origin is recent, and are scattered in areas that drain in different directions, suggesting movement by humans, rather than simply flowing water. Introduction of *P. cinnamomi* into previously uninfested areas along walking trails has been observed in Australia and Tasmania (Weste and Taylor 1971; Podger et al. 1990).

Most of the *P. cinnamomi* strains detected in *A. myrtifolia* habitat matched strains from agricultural and horticultural settings. Two of the four variants

have been in found in Christmas tree farms in the general area (Swiecki et al. 2005). Given that Christmas tree farms experience high volumes of traffic during December, when soils are usually wet, it is likely that *P. cinnamomi* could be transported to roadsides within *A. myrtifolia* habitat via infested soil clinging to tires. A third variant found at multiple mortality centers has been found previously associated with ornamental plants. Warnings about *P. cinnamomi* contaminating nursery stock date back at least to the 1950's (Gravatt 1954). Soil and/or water from infested ornamentals planted in local landscapes and diseased plant material dumped along roadsides (which we have observed in the area) represent potential avenues through which *P. cinnamomi* associated with container nursery plants may have been introduced into *A. myrtifolia* habitat.

Phytophthora cambivora *and* A. myrtifolia

An unexpected outcome of this survey effort was the identification of a second exotic and invasive soilborne *Phytophthora*, *P. cambivora* (Petri) Buisman, associated with root disease of *A. myrtifolia* and *A. viscida* on BLM property off Carbondale Road. *Phytophthora cambivora* is closely related to *P. cinnamomi*, and is also an aggressive root pathogen with a wide host range. *P. cambivora* is naturalized in parts of Europe, where it causes ink disease of *Castanea* Mill., and is pathogenic to *Quercus* L. species and *Fagus sylvatica* L. in forests. It also attacks nursery stock of various species in both Europe and the US. In some Oregon forests, *P. cambivora* causes a lethal canker disease of *Chrysolepis chrysophylla* (Hook.) Hjelmq. It also causes a collar rot of domesticated *Prunus* L. species (almonds and cherries), and *Malus pumila* Mill. in cultivation, and has been reported on *Abies procera* Rehder in Christmas tree farms in Washington.

Given that the area where *P. cambivora* was detected is distant from paved roads, the most likely sources of introduction are via off-road traffic along unpaved roads or via spore transport in a seasonal creek. A rural residential site has been developed directly north and upslope of the area where *P. cambivora* was detected, suggesting that contaminated nursery stock may have been the pathogen source.

MORTALITY CAUSED BY *PHYTOPHTHORA CINNAMOMI* IN OTHER NATURAL HABITATS

In August 2006, after discovery of *P. cinnamomi* in *A. myrtifolia* habitat, the first author was asked to investigate mortality of *A. pallida* Eastw. (a federal threatened species) in the Oakland Hills. *Phytophthora cinnamomi* was detected within a patch of dead and declining plants including *A. pallida* Eastw., *C. chrysophylla*, and other native species. The affected area was on a steep slope, a small distance downhill from a landscaped yard at a ridge top. The initial pathogen introduction was likely associated with nursery stock planted in the yard, with subsequent transmission resulting from downslope movement of infested water. Unfortunately, the mortality center was near the top of the watershed of the Huckleberry Regional Botanic Preserve, so further spread downslope into the preserve is inevitable.

As early as 2000, we had noted a patch of dead *Arctostaphylos* and dying *Arbutus menziesii* Pursh on a hillside where we had established a set of permanent sudden oak death (SOD) research plots in China Camp State Park. By 2000, this location had begun to develop high levels of mortality in *Quercus agrifolia* Née and *Q. kelloggii* Newberry due to the introduced SOD pathogen *Phytophthora ramorum* Werres, De Cock & Man in't Veld. However, species not normally killed by *P. ramorum* were also dead or dying in one portion of this SOD-affected location. In fall 2006, based on our experience with *A. pallida*, we identified an apparent root disease center covering more than 0.5 ha where both *A. menziesii* and *Umbellularia californica* (Hook. & Arn.) Nutt. were declining and dying. We recovered *P. cinnamomi* from soil beneath dead and dying *A. menziesii* and *U. californica* at multiple sites within this root disease center and subsequently confirmed that *P. cinnamomi* causes severe root rot in both of these species.

The China Camp mortality center was adjacent to a fire road that served as a trail and was used by logging vehicles in an earlier eucalyptus removal project. The road has since been closed and obliterated, partially in response to the threat posed by *P. cinnamomi.* Recreational use of trails by mountain bikers and hikers as well as downhill spread via flowing water are likely to spread *P. cinnamomi* more widely in the park. The combined effects of mortality due to *P. ramorum* and *P. cinnamomi* have the potential to devastate much of the mixed hardwood forest in the park.

Based on our experience at China Camp, we determined that the combination of dead and

declining *A. menziesii* and *U. californica* is a strong indicator of *P. cinnamomi* invasion in mixed hardwood forests. This has been borne out by subsequent detections. In 2007, we found another hardwood site affected by both *P. ramorum* and *P. cinnamomi* in Sonoma County near Valley Ford. We recovered *P. cinnamomi* from both soil and roots of declining and dying *U. californica* and *A. menziesii* at this site, where landscaping activity was the likely route of pathogen introduction. More recently, we recovered *P. cinnamomi* from soil in a large patch of dead and dying *A. menziesii* on an unpaved road upslope from the historic Filoli Estate in San Mateo County. Infested soil transported by vehicles from the Filoli gardens is the likely source of the introduction. Although the road is not public, it is used by vehicles that travel throughout the San Francisco Public Utilities Commission Peninsula Watershed, a large area that includes several rare *Arctostaphylos*: *A. regismontana* Eastw., *A. andersonii* A.Gray, and *A. montaraensis* J.B.Roof.

PRESENCE OF *PHYTOPHTHORA CINNAMOMI* IN PLANTS FROM NATIVE PLANT NURSERIES

Prior to our investigations *A. menziesii* and *U. californica* had not been reported as hosts of *P. cinnamomi*. We therefore conducted controlled pathogenicity tests using container-grown plants. These tests confirmed that *P. cinnamomi* can cause lethal root decay of both species. *Arctostaphylos menziesii* showed greater sensitivity to the pathogen than did *U. californica,* which was consistent with field observations.

While completing pathogenicity tests, we monitored nursery-reared *A. menziesii* for *Phytophthora* infestations. We purchased plants from four nurseries, all specializing in California native plants. Alarmingly, we found eight plant-pathogenic *Phytophthora* species associated with nursery-grown *A. menziesii*. Four *Phytophthora* species (*P. cryptogea* Pethybr. & Laff, *P. gonapodyides* (H.E. Petersen) Buisman, *P. nicotianae* Breda de Haan, *P. pseudosyrinagae* T. Jung & Delatour) were baited from potting soil, but not associated with root infections. *Phytophthora cactorum* (Lebert & Cohn) J. Schröt., *P. cambivora*, and *P. cinnamomi* were associated with root infections, and *P. syringae* (Berk.) Kleb. was associated with stem cankers. These results demonstrate that nurseries specializing in California native plants can have *Phytophthora* contamination problems similar to what has been seen among standard landscape plant nurseries.

What can be done?

The expanding list of wildland *P. cinnamomi* infestations may foreshadow a much wider invasion of California native habitats by *P. cinnamomi* and other exotic *Phytophthora* species. While the expanding SOD epidemic caused by *P. ramorum* has received significant attention from regulators, researchers, and the public, the degree of the threat posed by *P. cinnamomi* and other soil *Phytophthora* species to California's native vegetation has not been as widely recognized.

The initial introduction and spread of *P. ramorum* in California was associated with movement of contaminated nursery stock (Mascheretti et al. 2008), and efforts to prevent its spread beyond the infested zone in California and southern Oregon rely strongly on inspection, certification, and tracking of nursery stock. Similarly, it appears that contaminated nursery plants are a likely source of the *P. cinnamomi* infestations at several of the San Francisco Bay area sites discussed above, and at least some of the infestations in *A. myrtifolia* habitat. The common occurrence of *P. cinnamomi* and other root-rotting *Phytophthora* species in both native and exotic plant nursery stock poses a high risk of pathogen introduction to other native habitats. Plants used in landscaping around homes in the urban-wildland interface are an obvious risk factor, but the prevalence of *Phytophthora* species in native plant nursery stock suggests that plants used in restoration plantings could commonly introduce these pathogens into the wild.

It is possible to produce nursery plants free from *P. cinnamomi* and other *Phytophthora* species. The foundation for producing disease-free nursery plants relies on using pathogen-free soil, disease-free propagation stock, and following phytosanitary procedures throughout the entire propagation cycle. Unless a nursery rigorously observes all three principles, planting stock can easily become infested. Common routes by which nursery plants may become infested include the use of reclaimed and recirculated irrigation water and movement of infested soil via hoses, tools, pots, hands, shoes, and vehicles. To avoid contamination, pots and flats should never be placed on the ground. Benches, pots, tools, and other items used in the propagation process need to be routinely disinfested at the beginning of each use. The principles apply equally to large scale and small scale nurseries, including backyard propagators.

Any nursery stock infested with *Phytophthora* species should not be used in plantings in or adjacent

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to natural areas. However, there is currently no certification program to ensure that nursery stock is free of *Phytophthora*. Potential buyers of nursery stock, including organizations that contract for native plants to be used in restoration projects, need to conduct their own testing and inspect nursery facilities to see whether the cultural practices are sufficient to produce clean stock. Because the contamination risk increases the longer that a plant is held in the nursery, younger planting stock is less likely to be infested than is older stock. Additionally, the presence of *Phytophthora* contamination can be masked in fungicide-treated plants. Fungicide treatment can prevent disease symptoms but will not free plants and container soil of *Phytophthora* spores. Due to residual fungicide activity, plants of unknown quality should be held at least two months before testing for presence of *Phytophthora* species.

Due to the widespread presence of *P. cinnamomi* and other *Phytophthora* species in urban and agricultural environments and a growing number of wildland areas, the risk of pathogen spread via inadvertent soil movement is high. Soil on shoes, vehicle tires, and tools are known to be important means by which *Phytophthora* species are spread to new areas. Travel on unpaved roads and trails in at-risk habitats should be avoided when soils are wet. Shoes and tools should be free of soil and cleaned with an appropriate agent (such as isopropanol or diluted bleach) before entering or leaving native habitats. Vehicles should remain on pavement to avoid collecting mud and should be cleaned after leaving a potentially contaminated area.

Although such procedures may initially seem onerous, they have become a necessity given the high efficiency with which exotic organisms can be moved both across the landscape and around the world. Furthermore, routinely following a full range of phytosanitary practices can help minimize introductions of exotic weeds, insects, and other plant pathogens.

ACKNOWLEDGMENTS

This work was supported in part by funding from the California Department of Fish and Game to San Francisco State University and University of California, Berkeley. We thank Andrea Brauer, Greg Browne, Daniel Burmester, Elaine Fok, Al Franklin, Tom Gordon, George Hartwell, Barbara Holzman, Heather Mehl, Tiffany Meyer, Rod Olarte, David Rizzo, Amy Smith, and Terry Weist for their assistance with various aspects of this research.

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