Phytophthora pathogens threaten rare habitats and conservation plantings

Susan J. Frankel[1], Janice Alexander[2], Diana Benner[3], Janell Hillman[4] & Alisa Shor[5]

Abstract

Phytophthora pathogens are damaging native wildland vegetation including plants in restoration areas and botanic gardens. The infestations threaten some plants already designated as endangered and degrade high-value habitats. Pathogens are being introduced primarily via container plant nursery stock and, once established, they can spread to adjacent areas where plant species not previously exposed to pathogens may become infected. We review epidemics in California – caused by the sudden oak death pathogen *Phytophthora ramorum* Werres, De Cock & Man in 't Veld and the first USA detections of *P. tentaculata* Kröber & Marwitz*,* which occurred in native plant nurseries and restoration areas – as examples to illustrate these threats to conservation plantings.

Introduction

Phytophthora (order: Peronosporales; kingdom: Stramenopila) pathogens have increasingly been identified as associated with plant dieback and mortality in restoration areas (Bourret, 2018; Garbelotto *et al.,* 2018; Sims *et al.,* 2019), threatened and endangered species habitat (Swiecki *et al.,* 2018a), botanic gardens and wildlands in coastal California (Cobb *et al.,* 2017; Metz *et al.,* 2017) and southern Oregon (Goheen *et al.,* 2017). The pathways for *Phytophthora* and other pathogen introductions are not always known but often they arrive inadvertently on infested plants for planting (nursery stock) (Liebhold *et al*., 2012; Parke *et al.*, 2014; Jung *et al*., 2015; Swiecki *et al*., 2018b; Sims *et al.,* 2019). Once established, *Phytophthora* spp. have the potential to reduce growth, kill and cause other undesirable impacts on a wide variety of native or horticultural vegetation (Brasier *et al.,* 2004; Hansen 2007, 2011; Scott & Williams, 2014; Jung *et al.,* 2018).

In this review, we focus on the consequences of two pathogen introductions: the sudden oak death pathogen *Phytophthora ramorum* Werres, De Cock & Man in 't Veld, as it attacks new host species more than two decades after it was first discovered in California

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[1] Susan J. Frankel is a Plant Pathologist with the USDA Forest Service.
Address: Pacific Southwest Research Station, 800 Buchanan Street, Albany, CA 94710, USA.
Email: susan.frankel@usda.gov
[2] Janice Alexander is Outreach Specialist at University of California Cooperative Extension, Marin County.
Address: 1682 Novato Blvd # 150B, Novato, CA 94947, USA.
[3] Diana Benner is owner of the Watershed Nursery.
Address: 601 A Canal Blvd, Richmond, CA 94804, USA.
[4] Janell Hillman is Senior Biologist/Plant Ecologist at Santa Clara Valley Water District.
Address: 5750 Almaden Expressway, San Jose, CA 95118, USA.
[5] Alisa Shor is Director of Park Nurseries, Golden Gate National Parks Conservancy.
Address: 201 Fort Mason, San Francisco, CA 94123, USA.

(Rooney-Latham *et al.,* 2017), and the first detections in the USA of *P. tentaculata* Kröber & Marwitz, which occurred in California native plant nurseries and restoration plantings from 2012 to 2014 (Rooney-Latham *et al.*, 2015; Sims *et al.,* 2018).

Follow-up investigations of these epidemics revealed that *Phytophthora* pathogens are common in ornamental nurseries (Yakabe *et al.*, 2009; Parke *et al.,* 2014; Knaus *et al.,* 2015; Blomquist *et al.,* 2016) and, in California, native plant nurseries and are being introduced to new areas when outplanted (Sims *et al*., 2018; Rooney-Latham *et al*., 2019; Swiecki *et al*., 2019). Once established, *Phytophthora* pathogens may infest the site and often are very difficult to eradicate or curtail (Goheen *et al*., 2017; Valachovic *et al*., 2017).

We focus on invasions into conservation or mitigation plantings, such as rare plant habitats, botanic gardens or restoration areas. Since these plantings are designed to improve habitats, enhance biodiversity or expand plant populations with high conservation value, their failure degrades the natural resources that they aim to benefit. Taken together, these California plant pathogen introductions serve as evidence that without additional preventive measures to ensure nursery stock health, actions intended to sustain and protect species may be undermined. Efforts to retain remnant plant populations in botanic gardens or restoration areas can be destroyed if measures are not taken to ensure that plant pathogens are not introduced into rare habitats, or elsewhere, where they can eventually encroach into conservation plantings.

Wildland and restoration *Phytophthora* epidemics in California

The sudden oak death pathogen spreads from wildlands to rare plants

For more than 30 years, coastal California and Oregon landscapes have been under attack by the invasive sudden oak death pathogen, *Phytophthora ramorum*, where over 50 million trees have been killed, primarily *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H. Oh (tanoak) and *Quercus agrifolia* Née (coast live oak) (Rizzo *et al*., 2005; Frankel, 2008; Garbelotto & Hayden, 2012; California Oak Mortality Task Force (COMTF), 2018) (Fig. 1). The pathogen has been introduced several times, most likely on ornamental nursery stock; once established, it spread via windblown rain into adjacent forests, parks and gardens (Grünwald *et al*., 2008; Grünwald *et al.,* 2012). Unexpectedly, starting in 2015 after two decades of monitoring, several more plant species, including *Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmqvist (chinquapin), *Pickeringia montana* Nutt. ex Torr. & A. Gray (chaparral pea) and rare *Arctostaphylos* spp. Adans. (manzanitas) were recognised as hosts showing symptoms of dieback and mortality (COMTF, 2017; Rooney-Latham *et al*., 2017). Many of these plant hosts are endangered (US Fish and Wildlife Service, 1998) or threatened species (Calflora, 2019) and several of the invasions occurred in botanic garden collections. These detections demonstrate the detrimental effects that invasive pathogens can have on plant life. *P. ramorum* is known to infect over 100 plant species including hardwoods, conifers, shrubs, herbaceous plants and ferns (US Department of Agriculture, 2013). Its broad host range includes common plants, such as tanoak (Bowcutt, 2015), and, over time, rare plants in conservation plantings and remnant habitats have been found as symptomatic and infected, apparently exposed to inoculum from nearby infested forests (Davidson *et al.*, 2005; Hansen *et al*., 2008).

From 2015 to 2017, *Phytophthora ramorum* was first recognised on several rare, threatened or endangered manzanita species in wildlands and botanic gardens (Table 1). In maritime chaparral of Marin and San Mateo Counties infection was observed on *Arctostaphylos glandulosa* Eastw. (Eastwood manzanita), *A. virgata* Eastw. (Marin manzanita) (Rooney-Latham *et al.,* 2017) and *A. montaraensis* Roof (Montara manzanita) (Matteo Garbelotto, University of California, Berkeley, pers. comm.). Additionally, the pathogen infested plants in two botanic gardens. In the University of California, Santa Cruz Arboretum and Botanic Garden (Santa Cruz County), *P. ramorum* was detected on *A. hooveri* P.V. Wells (Hoover's manzanita), *A. montereyensis* Hoover (Toro manzanita), *A. morroensis* Wiesl. & Schreiber (Morro manzanita), *A. pilosula* Jeps. & Wiesl. (La Panza manzanita), *A. pumila* Nutt. (dune manzanita) and *A. silvicola* Jeps. (Bonny Doon manzanita) (Matteo Garbelotto, pers. comm.). The pathogen was also reported on multiple rare manzanita species at the East Bay Regional Park Botanic Garden in Tilden Park near Berkeley, CA (Alameda County) – further details will be published soon by the California Department of Food and Agriculture (Suzanne Rooney-Latham, CDFA, pers. comm.). Symptoms appeared as leaf spots, dieback or complete plant mortality. All the detections occurred in areas known to be infested with *P. ramorum* for several decades, but symptoms on manzanita species had not previously been reported.

Also on East Bay Regional Park District (EBRPD) lands, *Phytophthora ramorum* was found damaging *Arctostaphylos pallida* Eastw. (pallid manzanita), a state endangered plant. State law requires the EBRPD protect

Fig. 1 Sudden oak death of tanoak in Sonoma County, CA. Photo: Christopher Lee, California Department of Forestry and Fire Protection.

Scientific name	Location, Year	Reference
Arctostaphylos glandulosa	Wildland, Marin Co., 2015	Rooney-Latham *et al*., 2017
Arctostaphylos hooveri	Botanic Garden, Santa Cruz Co., 2017	Matteo Garbelotto, University of California, Berkeley, pers. comm.
Arctostaphylos montaraensis	Wildland, San Mateo Co., 2017	Matteo Garbelotto, University of California, Berkeley, pers. comm. Discovered in 2017 SOD Blitz survey.
Arctostaphylos montereyensis	Botanic Garden, Santa Cruz Co., 2017	Matteo Garbelotto, University of California, Berkeley, pers. comm.
Arctostaphylos morroensis	Botanic Garden, Santa Cruz Co., 2017	Matteo Garbelotto, University of California, Berkeley, pers. comm.
Arctostaphylos pallida	Wildland, Alameda Co., 2017	Swiecki *et al*., 2018a
Arctostaphylos pilosula	Botanic Garden, Santa Cruz Co., 2017	Matteo Garbelotto, University of California, Berkeley, pers. comm.
Arctostaphylos pumila	Botanic Garden, Santa Cruz Co., 2017	Matteo Garbelotto, University of California, Berkeley, pers. comm.
Arctostaphylos silvicola	Botanic Garden, Santa Cruz Co., 2017	Matteo Garbelotto, University of California, Berkeley, pers. comm.
Arctostaphylos virgata	Wildland, Marin Co., 2015	Rooney-Latham *et al*., 2017

Table 1 Partial list of *Arctostaphylos* spp. (manzanitas) showing symptoms of *P. ramorum* infection discovered in California since 2015. All the plants developed symptoms in natural conditions.

A. pallida populations while the EBRPD manages this maritime chaparral habitat in the wildland-urban interface for plant health and fire fuels management. In response, botanists and plant pathologists have inventoried the populations, surveyed for pathogens, removed invasive weeds and deposited seed of pallid manzanita in several banks (EBRPD, 2017; Hammond, 2018).

Oregon's *Phytophthora ramorum* infestation demonstrates how difficult this pathogen is to control in forests and that introductions on nursery plants continue despite quarantines. In Oregon, *P. ramorum* was first discovered in coastal south-west Oregon forests in Curry County in July 2001 (Goheen *et al*., 2002) and subsequently introduced again in 2008 and 2014 (Grünwald *et al*., 2016; Goheen *et al*., 2017). An interagency team conducted early detection monitoring and mandatory eradication from 2001 to 2012, which slowed but did not stop pathogen spread and intensification (Peterson *et al.,* 2015). As required by state regulations, infested trees and other host plants were cut and burned along with a buffer of adjacent vegetation (Goheen *et al.,* 2017). From 2009 to 2011, funding limitations resulted in a treatment backlog of many infestations near the centre of the quarantine area (Kanaskie *et al.,* 2017), which led to creation of a Generally Infested Area (GIA) in which eradication was no longer required by law (Kanaskie & Navarro, 2019). In the absence of eradication treatments within the GIA, tanoak mortality increased rapidly (Fig. 2). Oregon Department of Forestry reports that on ten 1-ha plots near Brookings, Oregon (Curry County), overstorey tanoak mortality increased from less than 5 per cent to an average of 87 per cent over a four-year period. Also from 2012 through 2017 the disease spread rapidly, and the untreated, infested area within the 151 sq. km GIA increased from 85 ha to more than 1,020 ha (Kanaskie & Navarro, 2019).

The threat of new *Phytophthora ramorum* infestations from nursery stock movement was demonstrated yet again in Oregon in 2015, where despite federal (7 CFR 301.92, US Department of Agriculture, 2002) and state (603-052-1230 and 603-052-1250, Oregon Department of Agriculture, 2001) quarantines, another, more aggressive lineage of the pathogen, the European Union 1 (EU1) clonal lineage, was detected as introduced for the first time into a USA forest, on tanoak located approximately 1.6 km from a small private nursery near the Pistol River (Curry County, Oregon) (Grünwald *et al*., 2016; Grünwald *et al*., 2019). The EU1 clonal lineage was also found in the nursery (Grünwald *et al.*, 2016). State-mandated eradication has been conducted on over 190 ha that harboured the EU1 lineage of *P. ramorum*, but the pathogen continues to spread (Navarro *et al*., 2019).

The Sudden Oak Death: Economic Assessment, conducted for the Oregon Department of Forestry concluded that if the current sudden oak death treatment regime

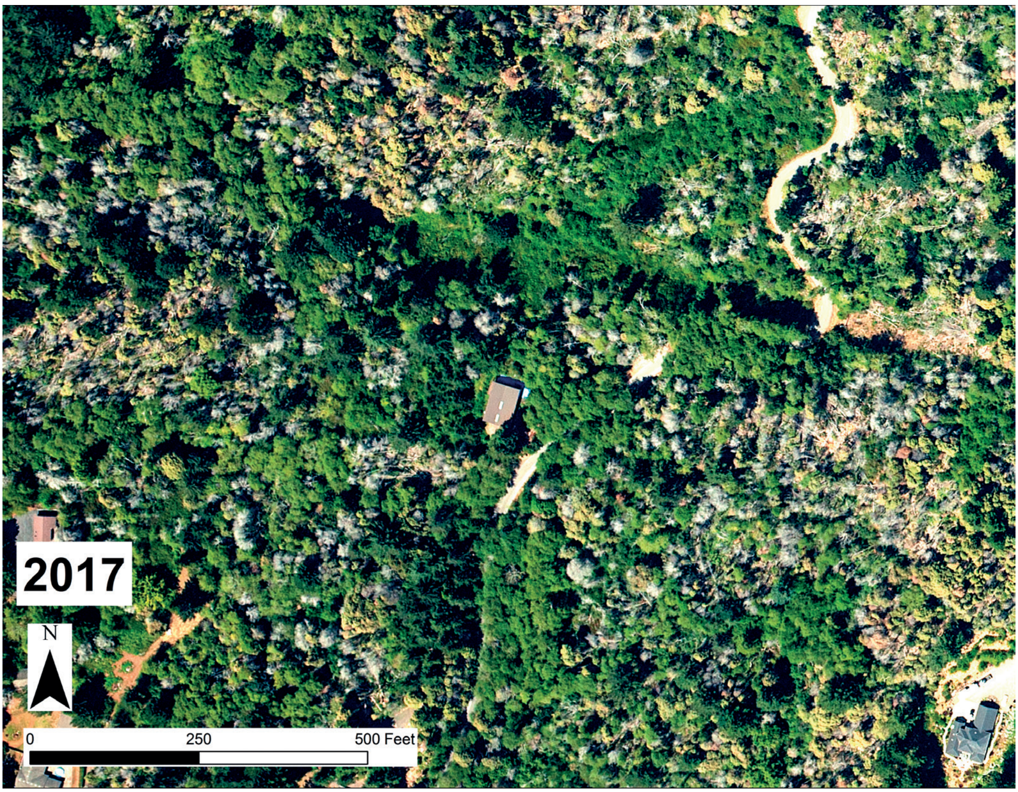

Fig. 2 Aerial view of mortality of dominant and co-dominant tanoaks killed by *Phytophthora ramorum* inside the Generally Infested Area near Brookings, OR. Photo: Oregon Department of Forestry.

(clear-cutting of infestations on the leading edge of disease expansion) was terminated, serious economic impacts might occur as *Phytophthora ramorum* moved north into Coos County (Highland Economics *et al*., 2019). Projected impacts included quarantines on south-west Oregon timber exports by China, Japan and Korea resulting in a loss of 1,200 jobs related to timber export, equal to $57.9 million in annual wages, as well as other losses in revenue from depressed property values and a decrease in tourism. The assessment also states that *P. ramorum* strikes at core values that elude economic quantification, particularly tribal cultural values (Highland Economics *et al*., 2019).

Fig. 3 *Phytophthora tentaculata* infected *Diplacus aurantiacus* (sticky monkey flower) in a restoration planting in Alameda County, CA, in 2014. Photo: Tedmund Swiecki, Phytosphere Research.

Phytophthora tentaculata *and other* Phytophthora *detections in California restoration areas and native plant nurseries*

Over the past five years, *Phytophthora* species have been introduced into restoration areas due to outplanting of infested nursery container plants (Garbelotto *et al*., 2018; Swiecki *et al*., 2018a, b; 2019). In 2012, *P. tentaculata* was discovered causing severe root and crown rot on *Diplacus aurantiacus* Jeps. (sticky monkey flower) at a native plant nursery in Monterey County and noted as a first USA detection (Rooney-Latham & Blomquist, 2014). In 2014, the pathogen was detected in five California native plant nurseries (Butte, Monterey, Placer, Santa Cruz Counties) and three habitat restoration sites in Monterey and Alameda Counties (Frankel *et al*., 2015) (Fig. 3). These detections shocked plant ecologists, as well as native plant growers, as evidence emerged that *P. tentaculata* had been unintentionally but extensively introduced into habitat restoration sites in the greater San Francisco Bay Area (Frankel *et al*., 2018; Garbelotto *et al*., 2018).

Several habitat restoration sites designed to serve as mitigation for municipal water infrastructure projects were inadvertently planted with *Phytophthora tentaculata* infected plants including *Frangula californica* (Eschsch.) A. Gray (coffeeberry), *Heteromeles arbutifolia* (Lindl.) M. Roem. (toyon) and others (Fig. 4). The plantings extended along several kilometres of riparian area at various locations in Alameda County (Lyman *et al*., 2017) (Fig. 4). In another first detection in the USA, *P. quercina* was found on a planted *Quercus lobata* Née (valley oak) in a restoration area in San Jose (Santa Clara

Fig. 4 Alameda County restoration site showing coloured flags noting locations of outplanted container nursery stock. Post-planting, the site tested positive for *Phytophthora*. Photo: Tedmund Swiecki, Phytosphere Research.

County) (Swiecki *et al*., 2018a). In 2009, both *P. quercina* and *P. tentaculata* were listed among the top five most threatening *Phytophthora* species, not yet detected in the USA, in an USDA Animal and Plant Health Inspection Service (APHIS) pest risk analysis (Schwartzburg *et al*., 2009), so plant ecologists were challenged with developing a means to contain these infestations.

In response to these soil-borne *Phytophthora* introductions, project managers suspended plantings, cancelled orders of nursery stock and invested millions of dollars in solarisation treatments to clean up contaminated sites. But such measures achieved only partial eradication (Hillman *et al*., 2017; Lyman *et al*., 2017). The California native plant nursery industry responded by voluntarily submitting samples to the California Department of Food and Agriculture diagnostic lab for *Phytophthora* testing. *Phytophthora* was confirmed from over three quarters (77 per cent) of the 26 participating nurseries, on 37 per cent of the 402 samples tested from plants in 22 host families (Rooney-Latham *et al*., 2019). Rooney-Latham *et al.* (2019) conclude that their findings "document the widespread occurrence of *Phytophthora* spp. in native plant nurseries and highlight the potential risks associated with outplanting infested nursery-grown stock into residential gardens and wildlands".

In 2015, recognising that neither discontinuation of restoration planting nor a switch to direct seeding represent an ideal long-term approach to *Phytophthora* prevention, we created the Phytophthoras in Native Habitats Work Group (the Work Group)[6] to develop best management

[6] See www.calphytos.org

practices and other recommendations to prevent further pathogen introductions and ensure that the benefits of restoration are not foregone or significantly delayed due to plant health risks.

The Work Group utilises an interdisciplinary, collaborative approach to bring together native plant growers, vegetation managers, restoration design and installation contractors, regulators and plant pathologists to address the potential for pathogen introduction in all phases of restoration from design to planting and site maintenance. The Work Group is currently conducting a pilot project, entitled "Accreditation to Improve Restoration and Native Plant Nursery Stock Cleanliness" (AIR), to promote sanitation and other preventive measures in restoration nurseries (Frankel *et al*., 2019; Swiecki *et al*., 2019). Eleven California nurseries have voluntarily enrolled and committed to a self-assessment followed by an external audit to confirm that they are producing plants with the practices outlined by the Work Group (2016) best management practices for restoration nursery stock. These practices require growers to dedicate a significant amount of time and attention to phytosanitation throughout their operations. The nursery assessment covers all aspects of nursery production, divided into 12 categories including layout, water source, media, propagation and sanitation practices.

To date, four nurseries have completed all the requirements and have been deemed "AIR compliant", valid for one year. However, in one of the participating nurseries in Sonoma County, as part of the voluntary inspection, auditors detected *Phytophthora pseudocryptogea* Safaief., Mostowf., G.E. Hardy & T.I. Burgess infection on an endangered species, *Oenothera deltoides* Torr. & Frém. ssp. *howellii* (Munz) W. Klein (Antioch Dunes evening primrose). The nursery is working to improve production practices to prevent future pathogen introductions. The virulence of *P. pseudocryptogea* on native plants is not fully known but it has been detected on *Arctostaphylos hookeri* G. Don ssp. *ravenii* P.V. Wells (Raven's manzanita) on federally managed lands of the Presidio (San Francisco, CA). Raven's manzanita is an endangered species; in the mid-1980s only one single plant existed (Rolston, 1985; Holloran, 1996). The plant has been cloned but some of the clones are suffering significant dieback due to *Phytophthora* infection as well as other pest problems (National Park Service, undated).

Conclusions

Examining the consequences of these plant pathogen epidemics demonstrates the importance of prevention to avert pathogen introductions to sustain and protect rare plants and habitats. Once introduced into landscapes, these pathogens are very difficult to impossible to control (Kanaskie & Navarro, 2019) and may cause damage to many high-value plants (Garbelotto *et al*., 2018). When environmental conditions are favourable, pathogens may spread through soil or water movement or via windblown rain and colonise numerous plant species (Eyre *et al*., 2013).

Nurseries are widely distributed throughout the US (Reichard *et al*., 2001) and their irrigated conditions are conducive to *Phytophthora* development (Swiecki *et al*., 2018b). Nursery production poses a risk for pathogen development and spread within and beyond their facilities via contaminated run-off or outplanted stock (Pérez-Sierra & Jung, 2013; Simamora *et al*., 2018; Weiland *et al*., 2018). Best management practices that emphasise strict phytosanitation can prevent pathogen development in nurseries (Sims *et* *al*., 2019), and thereby protect adjacent and distant natural areas.

Climate change and human population pressure are increasing the desire and need to restore at-risk and degraded ecosystems (Seddon *et al.,* 2014). Restoration plantings provide opportunities to reverse damage due to development, desertification or pollution as they slow biodiversity loss and enhance urban and wildland environments (Perring *et al.*, 2015). Due to environmental changes that limit plant species survival, restoration or conservation plantings may be the only way some species can grow and survive (Mounce *et al.*, 2017). However, introduced plant pathogens may impair efforts to conserve plant diversity as they can persist in the soil, making it unsuitable for plants (Swiecki *et al.,* 2018a). Prevention of invasive species introductions in all types of landscaping and restoration, whatever the scale, is an important part of protecting native habitats (Simamora *et al.*, 2018).

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