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Sudden Oak Death, *Phytophthora ramorum*: a Persistent Threat to Oaks and Other Tree Species

Susan J. Frankel, Plant Pathologist,
USDA Forest Service, Pacific Southwest Research Station,
800 Buchanan Street
Albany, CA 94710, USA
sfrankel@fs.fed.us

Katharine M. Palmieri, Public Information Officer
California Oak Mortality Task Force and California
Forest Pest Council
University of California Cooperative Extension
Berkeley, CA, 94720, USA
kpalmieri@berkeley.edu

ABSTRACT

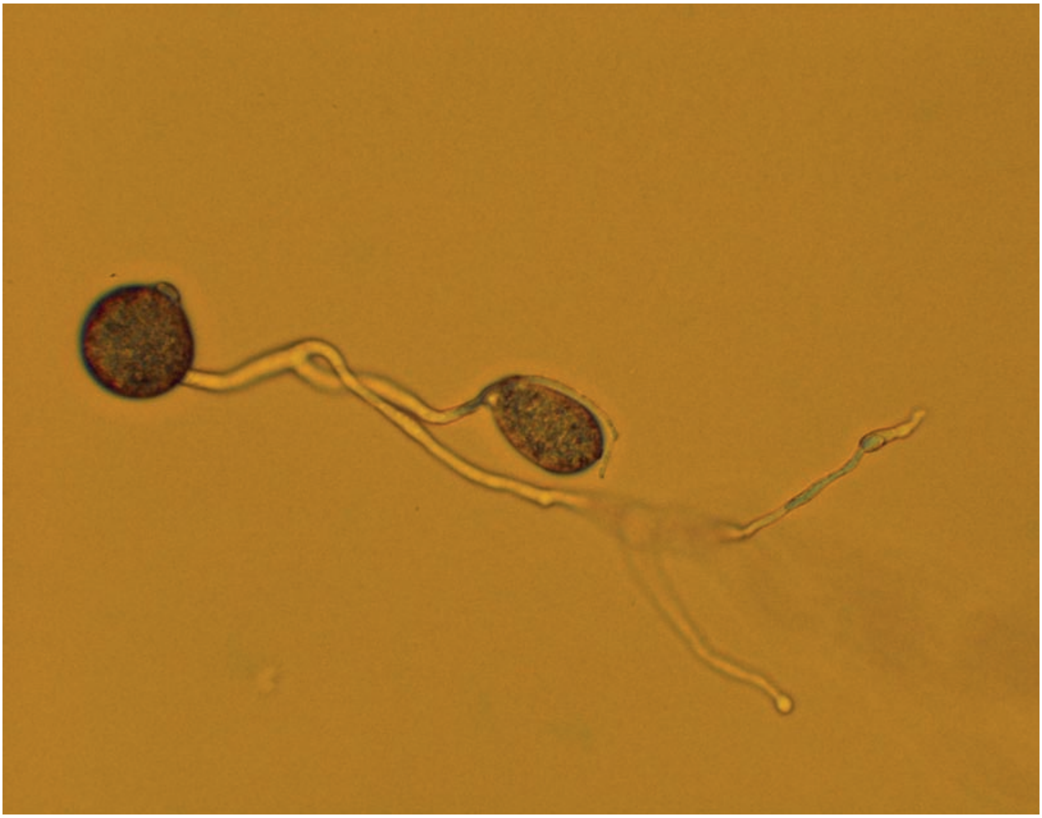
This paper reviews the status and management of sudden oak death and sudden larch death in the urban and wildland forests of California, Oregon, and the United Kingdom. The causal pathogen, *Phytophthora ramorum* (Werres, De Cock & Man in't Veld), was discovered in all three locations over a decade ago. Despite professional, dedicated attempts, efforts to contain and eliminate infestations have been unsuccessful. These less than satisfactory management intervention outcomes underscore the importance of prevention, for once forest pathogens become established, response is costly and difficult, and eradication is unlikely. New approaches are needed to protect forests from invasive pathogens.

Keywords: ***Notholithocarpus densiflorus, Quercus agrifolia, Larix kaempferi,*** **invasive forest pathogens, forestry management**

Introduction

Over the past 20 years, *Phytophthora ramorum* (Werres, De Cock & Man in't Veld), the pathogen known to cause sudden oak death, has killed well over 5 million trees along the coast of California and Oregon as well as millions of Japanese larch trees throughout much of the United Kingdom (UK) and areas of the Republic of Ireland. Despite eradication attempts and quarantines, four pathogen strains continue to move undetected overseas and across continents on nursery plant shipments (Goss et al., 2009; Grunwald et al., 2012). Meanwhile, in coastal California and Oregon, communities struggle to remove hazardous snags and reduce fuel loads as they lose tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H. Oh) and coast live oak (*Quercus agrifolia* Née) (Frankel, 2008). Additionally, in the UK, commercial Japanese larch (*Larix kaempferi* (Lamb.) Carrière) plantations are being clear-cut by the millions to comply with quarantine regulations and to slow pathogen spread (Brasier and Webber, 2010).

Sudden oak death is emblematic of the threat invasive species pose not only to oaks, but to the health of forest ecosystems. Here we present a review of the status and management of sudden oak death in the urban and wildland forests of California and Oregon and sudden larch death in the UK. In all three locations, determined, skillful efforts to eradicate or slow pathogen spread have not been fully realized; consequently, forests and the susceptible trees within them remain threatened. The less than satisfactory



1/ Chlamydospore of *Phytophthora ramorum* germinating on agar medium and forming a sporangium.

outcomes of management interventions underscore the importance of prevention, for once forest pathogens become established, response is costly and difficult, and eradication is unlikely.

Background

The pattern of mortality and symptoms of sudden oak death were first described in the mid-1990s (Rizzo et al., 2002), with *P. ramorum* identified as the causal agent several years later (Werres et al., 2001). A microscopic, fungus-like organism (Kingdom Stramenopila; phylum Oomycota) (Photo 1), the biology, genetics, and history of *P. ramorum* have been reviewed by Rizzo and Garbelotto (2003), Sansford et al. (2009), Kliejunas (2010), and Grunwald et al. (2008, 2012). The pathogen is currently known to infect over 135 plant species, with symptoms including leaf spots and/or twig dieback (USDA APHIS 2012) on all foliar or ramorum blight hosts and bleeding cankers and/or mortality on all sudden oak death or sudden larch death hosts, including coast live oak, California black oak (*Q. kelloggii* Newberry), Shreve oak (*Q. parvula* Greene var. *shrevei* (C.H. Mull.) Nixon), canyon live oak (*Q. chrysolepis* Liebm.), tanoak, and Japanese larch. With ramorum blight affecting common horticultural plants such as rhododendrons and camellias, the pathogen is able to inadvertently travel long distances via the movement of nursery stock (Ivors et al., 2006).

Once established in a susceptible forest, pathogen spread can occur through wind-driven rain, infested soil splash, watercourse currents, or by harvest and transport of infected plant material (Davidson et al., 2005). Cyclical in nature, the pathogen thrives in wet conditions, allowing inoculum build up and spread in years with ample moisture. Once a sudden oak death-susceptible tree is infected, its vascular system becomes obstructed, frequently leading to the death of the tree within a few years, when dry conditions lead to high evaporative demands (Brown and Brasier, 2007; Parke et al., 2007). However, not all infected trees die. Some oaks are able to form cankers that wall off and isolate the infection (Swiecki and Bernhardt, 2010).

An internationally recognized threat to forest ecosystems and the ornamental plant trade, *P. ramorum* quarantines have been initiated in Canada (2001), South Korea (2001), the US (2002), the UK (2002), Australia (2002), the EU (2002), the Czech Republic (2003), Taiwan (2006), New Zealand (2006), China (2008), and more than 65 other countries (COMTF, 2013; Sansford et al., 2009).

In the US, *P. ramorum* was detected at over 540 wholesale and retail nurseries between 2001 to 2013, with an average of 28 detections per year since 2007 (USDA APHIS, 2013). Detections for *P. ramorum* in the UK have averaged 50 sites per year from 2004 to 2013 in retail nurseries, garden centers, and plant passport nurseries. The average for the past seven years has been 37 sites per year (Jane Barbrook, personal communication, November 26, 2013).

Continental and global movement

Genetic analysis demonstrates that *P. ramorum* has moved across at least one ocean, become established, and infected native vegetation at least five times in North America and Europe (Grünwald et al., 2012; Van Poucke et al., 2012), with four clonal lineages having been identified in one or more locations. Each lineage (EU1, EU2, NA1, and

NA2) is named after the continent where it was first detected, followed by the number representing its order of discovery on that continent (Grünwald et al., 2009; Van Poucke et al., 2012).

The NA1 lineage was introduced to North America from an unknown location via imported nursery stock shipped to a nursery near Santa Cruz, CA sometime prior to the 1990s (Mascheretti et al., 2008, 2009; Grünwald et al., 2012). In 2004, millions of camellias potentially infected with the NA1 lineage were inadvertently shipped from a Los Angeles County, CA nursery to more than 1,200 nurseries in 39 states. The pathogen was ultimately recovered from 171 nurseries in 21 states (USDA APHIS 2013), and eventually detected in soil and water adjacent to infested nurseries in Alabama, Florida, Georgia, Mississippi, North Carolina, Washington, (Oak et al., 2013), Texas (COMTF 2013), and New York (Snover-Clift et al., 2013).

The NA2 lineage has been recovered from nurseries in Washington, California, and British Columbia, Canada as well as from waterways adjacent to infested nurseries in Washington and California. In spring 2009, runoff from a Pierce County, Washington retail nursery was the source of inoculum for salal (*Gaultheria shallon* Pursh) plants along a drainage ditch that became infected with the NA2 strain. The plants were destroyed and the pathogen has since only been recovered from the water in the drainage ditch (Chastagner et al., 2013).

The EU1 lineage was first detected in nurseries and established gardens in Germany and the Netherlands on *Rhododendron* and *Viburnum* in the 1990s (Werres et al., 2001). It was then discovered in the UK on *Viburnum* in 2002 (Lane et al., 2002) and on trees (*Q. falcata* Michx.) in 2003 in Sussex, southern Britain (Brasier et al., 2004) as well as in the Netherlands (*Q. rubra* L.). It continued to spread throughout the UK, sporulating on *R. ponticum* L. and threatening natural heathlands (Walters et al., 2009). Then, in 2009, Japanese larch emerged in the UK as a new host that both facilitated pathogen spread and died from infection (Brasier and Webber, 2010). The EU1 lineage has also been recovered from nurseries and adjacent waterways in California and Washington (COMTF, 2013).

The EU2 strain was first introduced to Northern Ireland and western Scotland in 2007 from Japanese larch, *Q. robur* L., *Vaccinium myrtillus*, L., and *R. ponticum*. Genetic analysis indicates it is a recent introduction, despite quarantine measures to prevent pathogen spread (Van Poucke et al., 2012).

Pathogen status in California

Sudden oak death continues to be the primary cause of tree mortality along 600 kilometers/373 miles of the California coast from Monterey County north to Humboldt County (Figure 1, Photo 2). Infestations occur in densely populated residential areas in several San Francisco Bay Area counties and in managed and unmanaged woodlands. The infestation is patchy and, due to an affinity for moisture, limited to areas within 80 kilometers/50 miles of the Pacific Ocean. Aerial surveys identified over 294,000 trees killed in 2013 alone, a number similar to mortality levels in 2012 (COMTF, 2013). In California, most of the mortality occurs in coastal evergreen forests with *Q. agrifolia*, California bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.), California black oak, Pacific madrone (*Arbutus menziesii* Pursh), and other species and in coast redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) forests with tanoak in the understory (Rizzo et al., 2002).

2/ Tanoaks killed by sudden oak death near Big Sur, Monterey Co., 2012.

Tanoak is the most susceptible species in California and Oregon. Some local populations in the Big Sur area (Monterey County, CA) have lost most of their mature tanoak trees because of sudden oak death (Cobb et al., 2012). Measurements in forest research plots in Marin County from 2000-2008 found approximately 78% (cumulatively) of all tanoak to be symptomatic, with a 51% mortality rate, while the cumulative infected rate for coast live oak was 50% with 32% mortality (McPherson et al., 2005; 2010). Swiecki and Bernhardt (2013) recorded cumulative mortality of coast live oak at 32% and tanoak mortality at 54% in Marin, Sonoma, and Napa County plots measured from 2000 to 2012. In all studies, the mortality rate for both species increased with tree size (McPherson et al., 2010; Cobb et al., 2012; 2013). Shreve oak, California black oak, canyon live oak, and Pacific madrone can also be killed by *P. ramorum* (Swiecki et al., 2013); however, as these species are not as common in infested areas, data on mortality rates is limited.

Despite widespread infestation throughout California's 14 infested counties, less than 10% of the native range of tanoak has been infected (Meentemeyer et al., 2012); however, mortality is expected to continue as the pathogen spreads north into the cool, moist environments of Northern California and coastal Oregon (Meentemeyer et al., 2011).

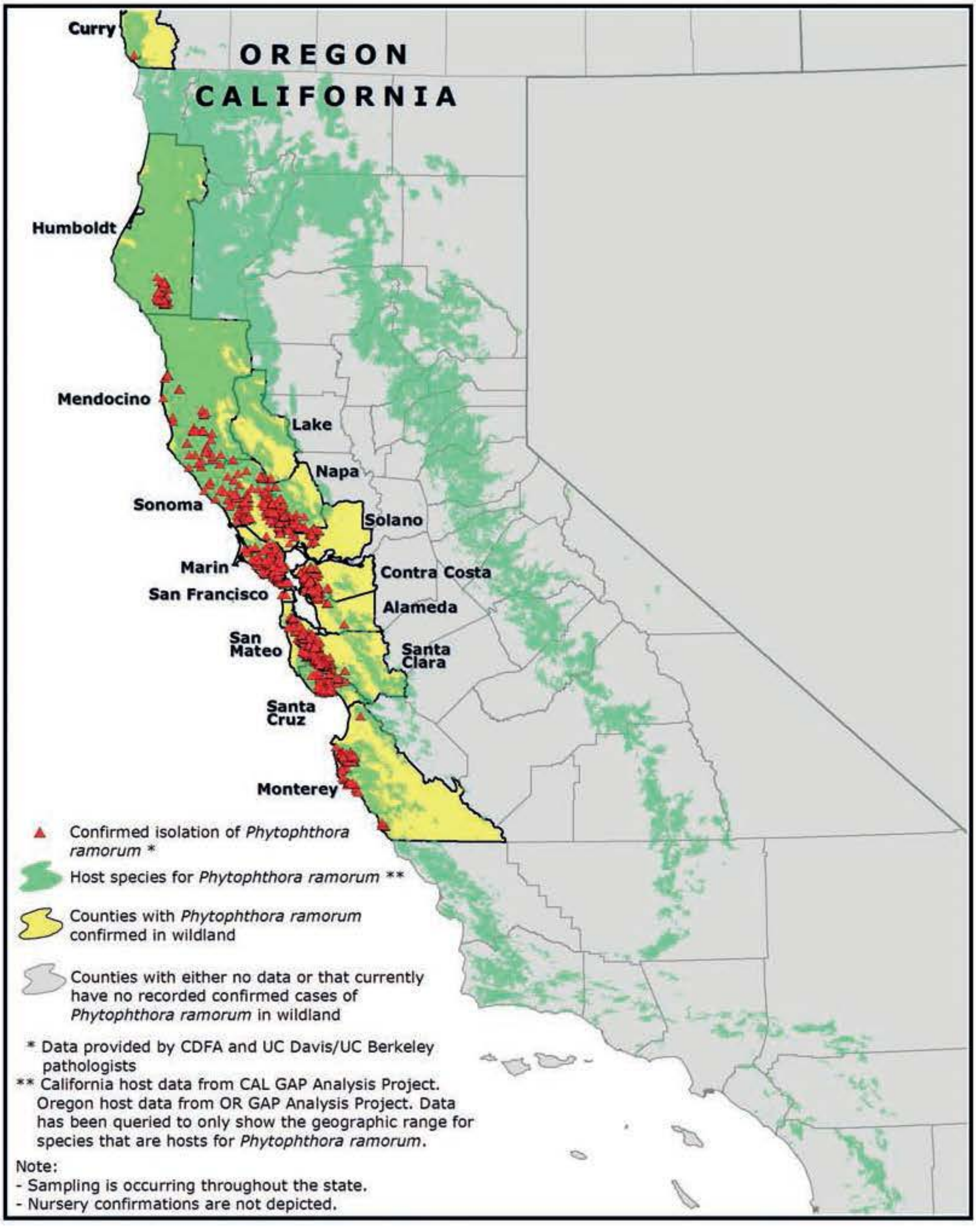


Figure 1/ Distribution of *Phytophthora ramorum* in California as of September 30, 2013. (Maggi Kelly, UC Berkeley, Geospatial Innovation Facility.)

Management in California

Widely dispersed in California by the time of its discovery in 2000 (Rizzo et al., 2002), sudden oak death management in the state has been focused on maintaining a safe environment, minimizing pathogen impacts in infested communities, and preventing long-distance movement of the pathogen (Frankel, 2008). Management is primarily locally driven, with landowners (individually or collaboratively) taking action in an effort to protect resources (Alexander and Lee, 2010). The non-profit California Oak Mortality Task Force (www.suddenoakdeath.org) works to coordinate sudden oak death-related activities as well as to provide educational outreach to impacted communities and industries, lawmakers, land managers, regulators, Native American tribes, and the media. As the state does not fund or require eradication, most management activity targets protecting individual high-value and/or high-risk trees, reducing roadside hazards from dead and failing trees, and abating fuels for fire prevention.

In 2011, an isolated outbreak 80 km/50 mi north of the nearest known California infestation was identified in Redwood Valley (Humboldt County, CA) and has been under eradication ever since. The infestation extended across more than 20 properties and included a mix of residential landholdings as well as large, private timberlands. Over 150 hectares/371 acres were treated with herbicide or by removal of infected trees and adjacent asymptomatic trees to create a 100 m/328 ft buffer. The multi-agency collaborative effort, led by University of California Cooperative Extension (UCCE), Humboldt and Del Norte Counties, relied on early detection and rapid response as the cornerstone of the eradication effort (Valachovic et al., 2013). However, despite treatment, wet springs led to pathogen spread into steep, rocky, densely vegetated terrain surrounding infested properties, which ultimately overwhelmed treatment efforts. As a result, the program is currently transitioning from eradication to a slow-the-spread or containment program. The pathogen continues to spread northward, threatening Redwood National and State Park as well as Yurok, Hoopa, and Karuk tribal lands.

Management in Oregon

In July 2001, *P. ramorum* was discovered in Curry County, Oregon. Since then it has spread across public and private lands in forests dominated by tanoak, with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and other tree species (Goheen et al., 2002; Hansen et al., 2008). A multi-agency team set out to eradicate the pathogen, with the state mandating that all infected trees as well as those within a 100 m/328 ft buffer be cut, piled, and burned on commercial timber lands, residential lots, parks, and federally managed forests. Although there was no direct cost to landowners, no compensation was made for loss of timber or other assets (Kanaskie et al., 2013).

Eradication sites were identified using fixed-wing airplanes and helicopters or by water baiting with native rhododendron and tanoak leaves (Sutton et al., 2009). These surveys were conducted by the Oregon Department of Forestry (ODF), Oregon State University, and Oregon Department of Agriculture in cooperation with the USDA Forest Service, and were followed by ground checks to confirm pathogen presence and identify newly infected trees for treatment (Kanaskie et al., 2013).

Over $10 million was expended from 2001 to 2012 to eradicate the pathogen in Oregon (Kanaskie et al., 2013) through a combination of federal and state funds. However,

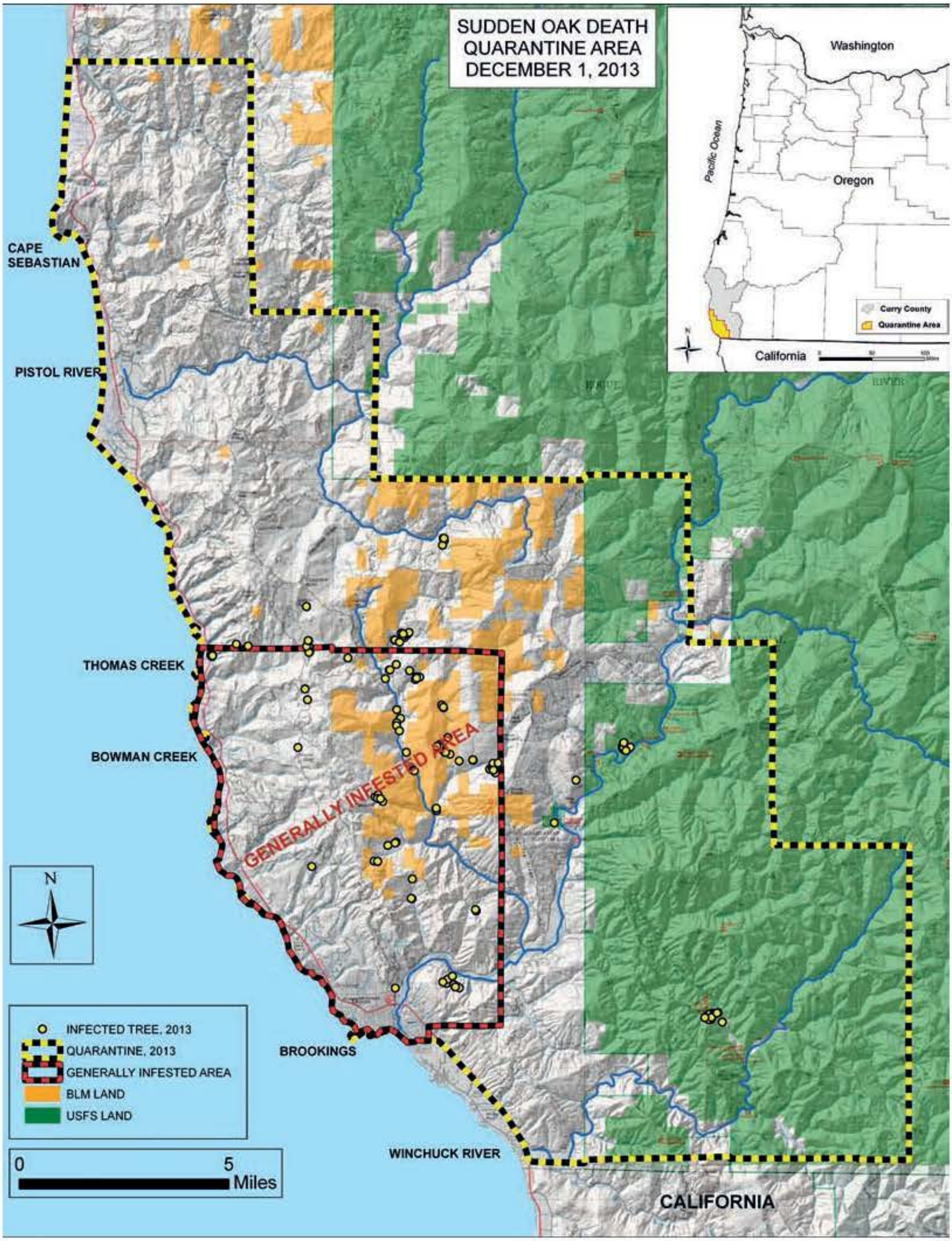


Figure 2/ Location of sites infested with *Phytophthora ramorum* in southwest Oregon that were discovered in 2013 (as of December 1). Sites enlarged for visibility. (Kanaskie, Oregon Department of Forestry.)

3/ Sudden oak death tanoak mortality near Brookings, Oregon inside the "Generally Infested Area" on private lands that are no longer under state-mandated eradication.

expansion and intensification of disease in late 2012 overwhelmed the funds and manpower required for treatment, making eradication unachievable. During the 10-year eradication effort, the pathogen spread from the initial infestation southward, 1.9 km/1.2 mi, and northward and eastward, 28 km/17.4 mi and 7.6 km/4.7 mi, respectively. The area under quarantine had expanded from 22 km^2/8.5 mi^2 in 2001 to over 680 km^2/263 mi^2 in 2013 (Figure 2). Eradication treatments eliminated the pathogen from 39% of the treated areas (Goheen et al., 2013), yet *P. ramorum* continued to slowly spread (predominantly northward, in the direction of storm tracks). Oregon revised its quarantine rule in March 2013, establishing a 125 km^2/48 mi^2 "Generally Infested Area" (GIA) where eradication is no longer required. Federal agencies continue to treat infestations on federal lands, but have redirected funds on private lands to focus on the leading edges of the infestation in an effort to slow disease spread and eradicate new, high-risk infestations. In the GIA, concern continues to grow over increased tree mortality posing hazardous conditions to people, dwellings, and roadways if standing dead trees and fuels are not removed (Photo 3).

Despite continued pathogen spread and disease intensification, Oregon's program has had numerous benefits. In the 12 years since the first detection, *P. ramorum* is still confined to a relatively small area of Curry County, OR, particularly when compared to similar areas in California that have only been managed for disease containment and slow-the-spread programs over the same period of time. This containment has protected wildlife and millions of tanoaks as well as shielded the Oregon nursery, forestry, and special products industries from quarantine restrictions.

Management in the United Kingdom

In 2002, a *P. ramorum* quarantine was initiated in England and Wales, limiting imports of host plants from California and Oregon as a precautionary measure whilst more evidence was gathered on pathogen risk (Sansford et al., 2010). At about the same time, the first UK *P. ramorum* find occurred on *Viburnum* at a garden center in Sussex, Britain (Lane et al., 2002). The pathogen continued to be intercepted in nurseries and historic gardens. From 2004 to 2013, approximately 446 retail and nursery confirmations were reported in England and Wales (Jane Barbrook, personal communication, November 26, 2013).

In spring 2009, a five year *Phytophthora* Disease Management Programme was launched by the UK Food Environment Research Agency (Fera) and the UK Forestry Commission (Walters et al., 2009). The program expanded research, education, and disease control through clearance of host plants in high-risk areas, with the goal of reducing inoculum to epidemiologically insignificant levels through the elimination of sporulating hosts (primarily *R. ponticum*). Then, in the summer of 2009 in Southwest England, Japanese larch was found to be a host of *P. ramorum*, supporting prolific pathogen sporulation as well as experiencing extensive dieback and mortality upon infection (Brasier and Webber, 2010). In 2010, *P. ramorum* was again isolated from larch plantations in Southern Wales, Northern Ireland, and the Republic of Ireland, and in 2011, it was found in Western Scotland (Schlenzig and Cooke, 2013). These infestations were the first widespread instances of lethal damage caused by *P. ramorum* to a commercially important conifer species anywhere in the world. In response to the larch detection, statutory Plant Health Notices were issued to woodland owners, requiring infected trees to be felled. Some financial assistance was offered through grants (UK Forestry Commission, 2012).

The impacts of the pathogen in the UK include the felling of millions of Japanese larch in commercial timber plantations, removing highly-valued rhododendron plants in historic gardens to maintain phytosanitary conditions, and costly impacts to the nursery industry for regulatory compliance (Sandsford et al., 2009). *P. ramorum* has also been found infecting bilberry, or European blueberry (*V. myrtillus* L.) (FERA 2012), in valuable, native lowland and upland heathlands.

Aerial surveys in spring 2013 detected a major disease expansion in the Dumfries and Galloway area of Scotland, where an estimated 4,000-6,000 hectares/9,884-14,826 acres of larch were infected (Forestry Commission - Scotland, 2013b.). This spread is believed to be a result of exceptionally wet and windy conditions in 2012 combined with the virulent genetic characteristics of the EU2 lineage. As a result, *P. ramorum* eradication on larch in Scotland was declared unachievable, causing the Scotland Forestry Commission to shift to a containment and slow-the-spread program. A proposed “red zone” (or generally infested area) in Southwest Scotland has been identified, delineating the area where the only statutory controls are movement of infested timber and bark. Statutory Plant Health Notices continue to be issued throughout the rest of Scotland, requiring felling or killing of infected stands of larch and all surrounding larch within 250 meters/820 feet (Forestry Commission - Scotland, 2013a).

Management hopes for the future

As the hope for eradication in each region struggling with *P. ramorum* dwindles, it is clear that this pathogen is one with which we must learn to live. Containing outbreaks to those regions currently infested is a primary goal if we are to protect natural resources, wildlands, and all the tangible and intangible benefits they provide. Tools to help minimize impacts from *P. ramorum* are relatively limited at this point. Educational outreach currently provides information to all affected parties on how to implement best management practices, thereby minimizing risk of artificial movement of the pathogen. Research into "super host" California bay laurel trees that may harbour disease even in the driest of years may also prove to be important in understanding and minimizing disease persistence in California (Eyre et al., 2013). Still even further off is the potential for disease management through deployment of naturally resistant tanoak stock as Hayden and others (2013) have identified tanoak traits and seedling families with increased survivorship and provided a framework to further identify seed parents for restoration.

Conclusions

While California, Oregon, and the UK have conditions unique to each region, such as climate, host species distribution, and pathogen lineage variation, the eradication actions in each area fell short of desired objectives. All three projects were conducted with state-of-the-art detection and treatment methods by capable, dedicated teams, yet, each program has only managed to slow disease spread while the pathogen continues to kill trees and expand into new areas. The experience gained from these eradication attempts has yielded many improvements in invasive species management: improved use of GIS databases and detection techniques as well as better preparation, coordination, and cooperation among forest managers, affected industry representatives, and regulatory agency personnel. But it has also demonstrated that complete eradication is likely not achievable as the pathogen is not identifiable early enough, leading to incomplete disease delimitation.

Unfortunately, throughout the 20th century similar scenarios have unfolded in Europe and North America with introductions of white pine blister rust (*Cronartium ribicola* A. Dietr.) (Liebhold et al., 2012), chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) (Freinkel, 2007), Dutch elm disease (*Ophiostoma ulmi* (Buisman) Nannf., *Ophiostoma novo-ulmi* Brasier) (Brasier, 1991), and other destructive forest pathogens. On average, two significant invasive forest pests are introduced into the US annually (Aukema et al., 2010). In Europe, invasive forest pathogens have increased exponentially in the last four decades, with approximately 60 pathogens introduced from the 1800s to the present (Santini et al., 2013). If society wants to protect trees, plants, natural resources, and industries from invasive species, additional ornamental nursery and forest research is needed to develop new approaches and technologies to prevent their introduction. Planning and action to protect against the next unknown pathogen is key to sustaining forests.

Photographers. Title page: Tom Coleman (dying tanoaks). Photo 1: Paul Tooley, USDA Agricultural Research Service. Photo 3: Tom Coleman, USDA Forest Service, Forest Health Protection. Photo 5: Ellen Goheen, USDA Forest Service.

Works cited

Alexander, J. and C.A. Lee. 2010. Lessons Learned from a Decade of Sudden Oak Death in California: Evaluating Local Management. *Environmental Management* 46(3): 315-328.

Aukema, J.E., D.G. McCullough, B. Von Holle, A.M. Liebhold, K. Britton, and S.J. Frankel. 2010. Historical Accumulation of Nonindigenous Forest Pests in the Continental US. *Bioscience* 60: 886-897.

Brasier, C.M., S. Denman, J. Rose, S.A. Kirk, K.J.D. Hughes, R.L. Griffin, C.R. Lane, A.J. Inman, and J.F. Webber. 2004. First report of ramorum bleeding canker on *Quercus falcata*, caused by *Phytophthora ramorum*. *Plant Pathology* 53: 804.

Brasier, C.M. 1991. *Ophiostoma novo-ulmi* sp. nov., causative agent of current Dutch elm disease pandemics. *Mycopathologia* 115(3): 151-161.

Brasier, C. and J. Webber. 2010. Plant pathology: sudden larch death. *Nature* 466: 824-825.

Brown, A.V. and C.M. Brasier. 2007. Colonization of tree xylem by *Phytophthora ramorum*, *P. kernoviae* and other *Phytophthora* species. *Plant Pathology* 56: 227-241.

California Oak Mortality Task Force [COMTF]. 2013. A chronology of *Phytophthora ramorum*, cause of sudden oak death and other foliar diseases http://www.suddenoakdeath.org/wp-content/uploads/2013/11/PRamorumChronology_11.06.131.pdf. 50 pages. (November 22, 2013)

Chastagner, G.A., K. Coats, and M. Elliott. 2013. An Overview of *Phytophthora ramorum* in Washington State. In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri, and J.M. Alexander. 2013. Proceedings of the Sudden Oak Death Fifth Science Symposium. Gen. Tech. Rep. PSW-GTR-243. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pgs. 14-15.

Cobb, R. C., J.A.N. Filipe, R.K. Meentemeyer, C.A. Gilligan, and D.M. Rizzo. 2012. Ecosystem transformation by emerging infectious forest disease: loss of large tanoak from California forests. *Journal of Ecology* 100: 712-722.

Cobb, R.C., D.M. Rizzo, K.J. Hayden, M. Garbelotto, J.A.N. Filipe, C.A. Gilligan, W.W. Dillon, R.K. Meentemeyer, Y.S. Valachovic, E. Goheen, T.J. Swiecki, E.M. Hansen, and S.J. Frankel. 2013. Biodiversity conservation in the face of dramatic forest disease: an integrated conservation strategy for tanoak (*Notholithocarpus densiflorus*) threatened by sudden oak death. *Madroño* 60(2): 151-164.

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

Eyre, C.A., M. Kozanitas, and M. Garbelotto. 2013. Population dynamics of aerial and terrestrial populations of *Phytophthora ramorum* in a California forest under different climatic conditions. *Phytopathology* 103: 1141-1152.

Forestry Commission, Scotland. 2013a. Action plan for ramorum on larch in Scotland (2013/14). 27 March 2013. 4 pages. http://www.forestry.gov.uk/pdf/FCSActionPlanforPramorum.pdf/$FILE/FCSActionPlanforPramorum.pdf. (November 22, 2013).

Forestry Commission, Scotland. 2013b. Latest updates on *Phytophthora ramorum*. August 2013. http://www.forestry.gov.uk/website/forestry.nsf/byunique/infd-9bglrr. (November 22, 2013)

Frankel, S.J. 2008. Sudden oak death and *Phytophthora ramorum* in the USA: A management challenge. *Australasian Plant Pathology* 37(1): 19-25.

Freinkel, S. 2007. American chestnut: the life, death, and rebirth of a perfect tree. University of California Press, Berkeley, CA.

Goheen, E.M., E.M. Hansen, A. Kanaskie, M.G. McWilliams, and W. Sutton, 2002. Sudden oak death caused by *Phytophthora ramorum* in Oregon. *Plant Disease* 86: 441.

Goheen, E.M., A. Kanaskie, E. Hansen, W. Sutton, P. Reeser, and N. Osterbauer. 2013. Monitoring the Effectiveness of *Phytophthora ramorum* Eradication Treatments in Oregon Tanoak Forests. In, In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri, J.M. Alexander. 2013. Proceedings of the Sudden Oak Death Fifth Science Symposium. Gen. Tech. Rep. PSW-GTR-243. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pg. 119.

Goss, E.M., M. Larsen, G.A. Chastagner, D.R. Givens, and N.J. Grünwald. 2009. Population Genetic Analysis Infers Migration Pathways of *Phytophthora ramorum* in US Nurseries. *PLoS Pathog* 5(9): e1000583.

Grünwald, N.J., M. Garbelotto, E.M. Goss, K. Heungens, and S. Prospero. 2012. Emergence of the sudden oak death pathogen *Phytophthora ramorum*. *Trends in Microbiology* 20: 131-138.

Grünwald, N.J., E.M. Goss, K. Ivors, M. Garbelotto, F.N. Martin, S. Prospero, E. Hansen, P.J.M. Bonants, R.C. Hamelin, G. Chastagner, S. Werres, D.M. Rizzo, G. Abad, P. Beales, G.J. Bilodeau, C.L. Blomquist, C. Brasier, S.C. Brière, A. Chandelier, J.M. Davidson, S. Denman, M. Elliott, S.J. Frankel, E.M. Goheen, H. de Gruyter, K. Heungens, D. James, A. Kanaskie, M.G. McWilliams, W. Man in 't Veld, E. Moralejo, N.K. Osterbauer, M.E. Palm, J.L. Parke, A.M. Perez Sierra, S.F. Shamoun, N. Shishkoff, P.W. Tooley, A.M. Vettraino, J. Webber, and T.L. Widmer. 2009. Standardizing the nomenclature for clonal lineages of the sudden oak death pathogen, *Phytophthora ramorum*. *Phytopathology* 99: 792-795.

Grünwald N.J., E.M. Goss, and C.M. Press. 2008. *Phytophthora ramorum*: a pathogen with a remarkably wide host range causing sudden oak death on oaks and ramorum blight on woody ornamentals. *Molecular Plant Pathology* 9: 729-40.

Hansen, E.M., A. Kanaskie, S. Prospero, M. McWilliams, E.M. Goheen, N. Osterbauer, P. Reeser, and W. Sutton. 2008. Epidemiology of *Phytophthora ramorum* in Oregon tanoak forests. *Canadian Journal of Forest Research* 38: 1133-1143.

Hayden, K.J., M. Garbelotto, R. Dodd, and J.W. Wright. 2013. Scaling up from Greenhouse Resistance to Fitness in the Field for a Host of an Emerging Forest Disease. *Evolutionary Applications* 6 (6): 970-982.

Ivors, K., M. Garbelotto, I. D.E. Vries, C. Ruyter-Spira, B. TE. Heckkert, N. Rosenzweig, and P. Bonants. 2006. Microsatellite markers identify three lineages of *Phytophthora ramorum* in US nurseries, yet single lineages in US forest and European nursery populations. *Mol. Ecol.* 15: 1493-1505.

Kanaskie, A., E. Hansen, E.M. Goheen, N. Osterbauer, M. McWilliams, J. Laine, M. Thompson, S. Savona, H. Timeus, B. Woosley, R. Wiese, W. Sutton, P. Reeser, J. Hulbert, R. Shultz, and D. Hilburn. 2013. Detection and Eradication of *Phytophthora ramorum* From Oregon Forests, 2001-2011. In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri, and J.M. Alexander. 2013. Proceedings of the Sudden Oak Death Fifth Science Symposium. Gen. Tech. Rep. PSW-GTR-243. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pgs. 3- 13.

Kliejunas, J.T. 2010. Sudden oak death and *Phytophthora ramorum*: A summary of the literature. Gen. Tech. Rep. PSW-GTR-234. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 181 p. http://www.fs.fed.us/psw/publications/documents/psw_gtr234/.

Lane, C.R., P.A. Beales, K.J.D. Hughes, R.L. Griffin, D. Munro, C.J. Brasier, and J.F. Webber. 2002. First outbreak of *Phytophthora ramorum* in England, on *Viburnum tinus*. *New Disease Reports* 6(13).

Liebhold, A.M., E.G. Brockerhoff, L.J. Garrett, J.L. Parke, and K.O. Britton. 2012. Live plant imports: the major pathway for forest insect and pathogen invasions of the US. *Frontiers in Ecology and the Environment* 10: 135-143.

Mascheretti, S., P.J.P. Croucher, M. Kozanitas, L. Baker, and M. Garbelotto. 2009. Genetic epidemiology of the sudden oak death pathogen *Phytophthora ramorum* in California. *Mol. Ecol.* 18: 4577-4590.

Mascheretti, S., P.J.P. Croucher, A. Vettraino, S. Prospero, and M. Garbelotto. 2008. Reconstruction of the Sudden Oak Death epidemic in California through microsatellite analysis of the pathogen *Phytophthora ramorum*. *Mol. Ecol.* 17: 2755-2768.

McPherson, B.A., S.R. Mori, D.L. Wood, A.J. Storer, P. Svihra, N.M. Kelly, R.B. Standiford, 2005. Sudden oak death in California: disease progression in oaks and tanoaks. *Forest Ecology and Management* 213: 71-89.

McPherson, B.A., D.L. Wood, S.R. Mori, N.M. Kelly, A.J. Storer, P. Svihra, and R.B. Standiford. 2010. Survival of oaks and tanoaks after eight years of sudden oak death monitoring in coastal California. *Forest Ecology and Management* 259: 2248-2255.

Meentemeyer, R.K., N.J. Cunniffe, A.R. Cook, J.A.N. Filipe, R.D. Hunter, D.M. Rizzo, and C.A. Gilligan. 2011. Epidemiological modeling of invasion in heterogeneous landscapes: spread of sudden oak death in California (1990–2030). *Ecosphere* 2(2): Article 17.

Meentemeyer, R.K., S.E. Haas, and T. Vaclavik. 2012. Landscape epidemiology of emerging infectious diseases in natural and human-altered ecosystems. *Annual Review of Phytopathology* 50: 379-402.

Oak, S., J. Hwang, and S. Jeffers. 2013. Comparison of In Situ and In Vitro Baiting Assays for *Phytophthora ramorum* Survey of Waterways in the Southeastern United States. In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri, and J.M. Alexander. 2013. Proceedings of the Sudden Oak Death Fifth Science Symposium. Gen. Tech. Rep. PSW-GTR-243. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pgs. 51-52.

Parke, J.L., E. Oh, S. Voelker, E.M. Hansen, G. Buckles, and B. Lachenbruch. 2007. *Phytophthora ramorum* colonizes tanoak xylem and is associated with reduced stem water transport. *Phytopathology* 97: 1558-1567.

Rizzo, D.M. and M.Garbelotto, 2003. Sudden oak death: endangering California and Oregon forest ecosystems. *Frontiers in Ecology and the Environment* 1: 197-204.

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

Sansford, C.E., A.J. Inman, R. Baker, C. Brasier, S. Frankel, J. de Gruyter, C. Husson, H. Kehlenbeck, G. Kessel, E. Moralejo, M. Steeghs, J. Webber, and S. Werres, S. 2009. Report on the risk of entry, establishment, spread and socio-economic loss and environmental impact and the appropriate level of management for *Phytophthora ramorum* for the EU. Deliverable report 28, York, UK: Forest Research, Central Science Laboratory . EU Sixth Framework Project RAPRA. 310 p. http://rapra.csl.gov.uk/ (November 22, 2013).

Sansford, C., A. Inman, and J. Webber. 2010. Development of a Pest Risk Analysis for *Phytophthora ramorum* for the European Union; the Key Deliverable from the EU Funded Project RAPRA. In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri. 2010. Proceedings of the Sudden Oak Death Fourth Science Symposium. Gen. Tech. Rep. PSW-GTR-229. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pages 139 – 153.

Santini, A., L. Ghelardini, C. De Pace, M.L. Desprez-Loustau, P. Capretti, A. Chandelier, T. Cech, D. Chira, S. Diamandis, T. Gaitniekis, J. Hantula, O. Holdenrieder, L. Jankovsky, T. Jung, D. Jurc, T. Kirisits, A. Kunca, V. Lygis, M. Malecka, B. Marcais, S. Schmitz, J. Schumacher, H. Solheim, A. Solla, I. Szabò, P. Tsopelas, A. Vannini, A.M. Vettraino, J. Webber, S. Woodward, and J. Stenlid. 2013. Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytologist* 197(1): 238-250.

Schlenzig, A. and D. Cooke. 2013. Genetic Diversity of *Phytophthora ramorum* in Nursery Trade and Managed Environment in Scotland. In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri, and J.M. Alexander. 2013. Proceedings of the Sudden Oak Death Fifth Science Symposium. Gen. Tech. Rep. PSW-GTR-243. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pgs. 33 – 39.

Snover-Clift, K.L., M.L. Daughtrey, M. Swartwood Towne, K. King, and M. Kelly. 2013. Initial detection of *Phytophthora ramorum* at two New York nurseries through sampling of water in retention ponds. *Phytopathology* 103(S2): 136.

Sutton, W., E.M. Hansen, P.W. Reeser, and A. Kanaskie, 2009. Stream monitoring for detection of *Phytophthora ramorum* in Oregon tanoak forests. *Plant Disease* 93: 1182-1186.

Swiecki, T.J. and E. Bernhardt. 2010. Long-Term Trends in Coast Live Oak and Tanoak Stands Affected by *Phytophthora ramorum* Canker (Sudden Oak Death). In, Frankel, S.J., J.T. Kliejunas, and K.M. Palmieri. 2010. Proceedings of the Sudden Oak Death Fourth Science Symposium. Gen. Tech. Rep. PSW-GTR-229. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pgs. 207-209.

Swiecki, T.J. and Bernhardt, E.A. 2013. A reference manual for managing sudden oak death in California. Gen. Tech. Rep. PSW-GTR-242. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 128 pgs.

Swiecki, T.J., E. Bernhardt, K. Aram, and D. Rizzo. 2013. Diagnosis and Management of *Phytophthora ramorum* Canker in Canyon Live Oak, an Atypical Bole Canker Host. In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri, and J.M. Alexander. 2013. Proceedings of the Sudden Oak Death Fifth Science Symposium. Gen. Tech. Rep. PSW-GTR-243. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pgs. 80-83.

UK Food and Environment Research Agency [FERA]. 2012. *Phytophthora ramorum* and *Phytophthora kernoviae* diseases on bilberry (*Vaccinium myrtillus*). A threat to our woodlands, heathlands and historic gardens. Plant Disease Fact Sheet. 4 pgs. http://www.fera.defra.gov.uk/plants/publications/documents/factsheets/phytophthoraBilberry.pdf. (November 22, 2013)

UK Forestry Commission. 2012. *Phytophthora ramorum* in larch trees - Update

30 July. http://www.forestry.gov.uk/forestry/INFD-8EJKP4. (November 22, 2013)

U.S. Department of Agriculture, Animal and Plant Health Inspection Service [USDA APHIS]. 2012. List of Regulated Hosts and Plants Proven or Associated with *Phytophthora ramorum* (January 2012). http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/pdf_files/usdaprlist.pdf

(November 22, 2013).

U.S. Department of Agriculture, Animal and Plant Health Inspection Service [USDA APHIS]. 2013. APHIS *Phytophthora ramorum* Program 2013, 2nd Quarter Summary. June 30. http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/updates/2013/2nd-Qtr-2013.pdf. (November 22, 2013)

Van Poucke, K., S. Franceschini, J.F. Webber, A. Vercauteren, J.A. Turner, A.R. McCracken, K. Heungens, and C.M. Brasier. 2012. Discovery of a fourth evolutionary lineage of *Phytophthora ramorum*: EU2. *Fungal Biol.* 116(11): 1178-91.

Walters, K., C. Sansford, and D. Slawson. 2009. *Phytophthora ramorum* and *Phytophthora kernoviae* in England and Wales - Public Consultation and New Programme. In: Frankel, S.J., J.T. Kliejunas, and K.M. Palmieri. Proceedings of the sudden oak death fourth science symposium. Gen. Tech. Rep. PSW-GTR-229. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. Pages 6-14.

Werres, S., R. Marwitz, W.A. Man in ‘t Veld, A.W. De Cock, P.J.M. Bonants, M. De Weerdt, K. Themann, E. Ilieva, and R.P. Baayen. 2001. *Phytophthora ramorum* sp. nov: a new pathogen on *Rhododendron* and *Viburnum*. *Mycological Research* 105(10): 1155-1165.

Valachovic, Y., L. Quinn-Davidson, C. Lee, E. Goldsworthy, and P. Cannon. 2013. Novel Approaches to SOD Management in California Wildlands: A Case Study of “Eradication” and Collaboration in Redwood Valley. In, Frankel, S.J., J.T. Kliejunas, K.M. Palmieri, and J.M. Alexander. 2013. Proceedings of the Sudden Oak Death Fifth Science Symposium. Gen. Tech. Rep. PSW-GTR-243. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Pgs 99-107.

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