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Sudden oak death and *Phytophthora ramorum* in the USA: a management challenge

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Abstract. Oaks and tanoaks in California and Oregon coastal forests are being ravaged by sudden oak death. The exotic causal agent, *Phytophthora ramorum*, is an oomycete in the Straminipile group, a relative of diatoms and algae. *P. ramorum* also infects many popular horticultural plants (i.e. camellia and rhododendron), causing ramorum blight, with symptoms expressed as leaf spots, twig blight and shoot dieback. *P. ramorum* has raised important biosecurity issues, which continue to reverberate through the agriculture, forestry and horticulture industries as well as associated government management, regulatory and scientific agencies. The continued spread of this and other new *Phytophthora* spp. presents significant impetus for adjustments in the management and regulation of forest pathogens and nursery stock.

History and background

Sudden oak death was first observed in the San Francisco Bay Area of California (CA), in the United States (US), in the mid-1990s. However, it was not until the summer of 2000 when the causal agent, now known as *Phytophthora ramorum* (Werres, Cock & Man in't Veld), was isolated. At the time of discovery, the pathogen was thought to be new to science. However, a few months later, Clive Brasier, from United Kingdom (UK) Forestry Research, recognised that an unnamed *Phytophthora* culture isolated in 1993 from blighted rhododendrons in Germany was morphologically identical. While the origin of the pathogen remains unknown, it has been determined that the European population and the North American wildland population are distinct from one another, yet descendents from a common ancestral population.

In CA, the sudden oak death epidemic erupted in 1995, killing tanoak (*Lithocarpus densiflorus*) in yards and open space areas where 6 million people live. Tanoaks are a common, nondescript tree, considered weeds by foresters managing commercial forest stands where it competes with redwood (*Sequoia sempervirons*) and Douglas-fir (*Pseudotsuga menziesii*). Consequently, there was little concern over the unusual pattern of tanoak mortality until 1998, when prized coast live oak (*Quercus agrifolia*), a symbol of the natural beauty of CA, were also observed dying in large numbers. By then, the pathogen had been found scattered across six CA counties, from Big Sur, Monterey County to Sonoma County, spanning more than 250 km of the central CA coast (Fig. 1).

P. ramorum has a broad host range, with hardwoods, conifers, shrubs, herbaceous plants, and ferns all known to be susceptible. Although the host list currently includes 109 species, infection rarely leads to mortality for hosts other than oak or tanoak. A host list is maintained by the US Department of Agriculture's (USDA) Animal and Plant Health Inspection Service (APHIS). It can be found at http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/pdf_files/usdaprlist.pdf (accessed 15 November 2007).

Nursery detection and regulatory action

P. ramorum was first confirmed in a US nursery in 2001 at a commercial facility in Santa Cruz County, CA, on rhododendron container plants (COMTF 2007*a*). Surrounded by forest land, the nursery owner had reported recent die-off of coast live oak, Shreve oak (*Q. parvula*) and tanoak surrounding the property (Musitelli 1999). Native CA bay laurel trees, an important sporulating host for *P. ramorum*, were also common in and surrounding the nursery. Follow-up water baiting efforts also recovered the pathogen in the waterways adjacent to the nursery (Tjosvold *et al*. 2002).

The first *P. ramorum* quarantine was issued in early 2001 by the State of Oregon (OR). It banned host plants and host plant products coming from CA unless they had been treated. A few months later (9 March 2001), Canada issued a similar quarantine, which prohibited the import of nursery stock and unmanufactured, non-propagative material (such as logs and mulch) of all oaks, tanoak, *Rhododendron* spp. and evergreen huckleberry (*Vaccinium ovatum*), as well as soil from areas where sudden oak death had been found. In the spring of 2001, the CA Board of Forestry declared a 'zone of infestation' for the seven counties (Santa Clara, Marin, Sonoma, Napa, Santa Cruz, San Mateo, and Monterey) known to be naturally infested with *P. ramorum*. The creation of the zone allowed the CA Department of Forestry and Fire Protection to regulate during timber harvest and management activities. Then, on 17 May 2001, the CA

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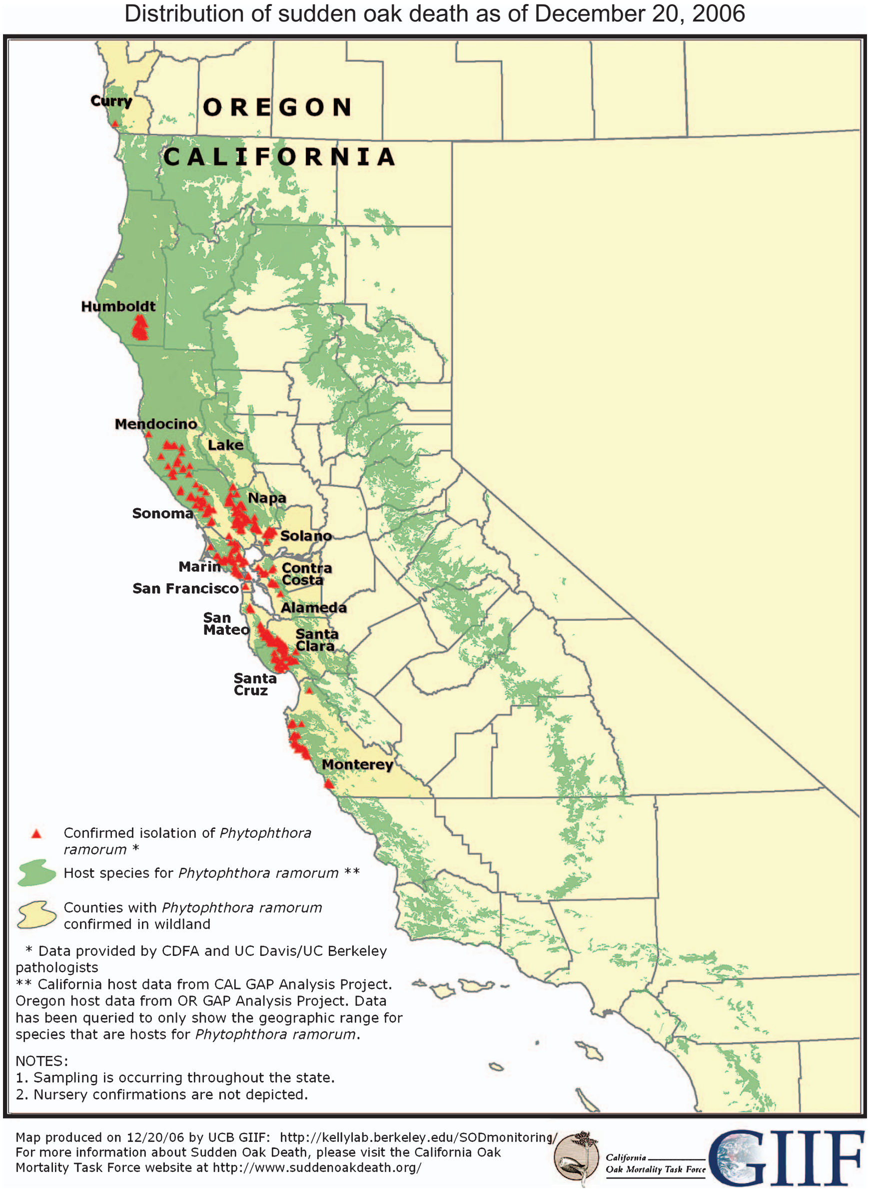

Fig. 1. Distribution of *Phytophthora ramorum* in wildlands in the United States.

Department of Food and Agriculture (CDFA) issued emergency regulations that restricted the export of diseased oak products and rhododendrons from each of the seven infested counties. The USDA APHIS followed by issuing an interim federal regulation (7 CFR Part 301) on 14 February 2002 for domestic interstate movement of *P. ramorum* host material from the CA counties known to be infested. International regulations were also enacted, with the European Union (EU) adopting emergency measures (2002/757/EC), as well as Canada, the UK, South Korea, New Zealand, Australia, the Czech Republic, Mexico, Taiwan and the US. (Kliejunas 2007).

In 2003, infested container nursery stock was detected at 20 nurseries in British Columbia, OR, Washington (WA), and CA; regulatory action was taken to eradicate the pathogen (Alexander 2006). In the winter of 2003, *Camellia* was first detected as a host in 15 UK nurseries and three public gardens (Beales *et al.* 2004). Shortly thereafter, infected *Camellia* container plants were detected in a nursery in Santa Cruz County, CA on stock that had been delivered from a nursery in Stanislaus County, CA (~167 km inland). The originating Stanislaus County nursery was surrounded by pasture, distant from the infested forest areas and in a significantly hotter climate.

The detections in a smattering of nurseries, far from infested forests and in variable climates, did not portend the March 2004 *P. ramorum* detections in two large southern CA nurseries and one in OR. In 2004, the US quarantine targeted risks associated with wildlands and nurseries within naturally infested counties; consequently, nurseries outside of those counties were not regulated. The Southern CA nursery detections were made as part of the *P. ramorum* National Nursery Survey and also a trace-back investigation from a WA nursery found positive for the pathogen. These large nurseries had shipped millions of potentially infected plants to over 1200 nurseries in 39 states. Within a month, 15 states imposed quarantines on CA nursery stock. Some states imposed an outright ban on all CA nursery stock shipments. The financial impacts were devastating, with an estimated loss of US $4.3 million to CA's nursery industry in March alone. In response, the USDA APHIS issued an emergency order quarantining all nurseries with host plants in Washington, OR, and CA. Expenditures for USDA APHIS-funded regulatory action to find and destroy all infested stock rose to US$20 million that year (United States Government Accountability Office 2006). By the end of 2004, the pathogen was recovered in 20 states, with 171 nursery-related detections (Cooperative Agriculture Pest Survey Program 2005).

The protocols, regulated articles and scope of the US federal regulations may be found on the USDA APHIS *P. ramorum* website http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/index.shtml (accessed 15 November 2007).

Oregon wildland and nurseries

Alerted to the problem in CA, OR forest pathologists conducted roadside and aerial surveys of high-risk tanoak in the summer of 2000. In July 2001, an aerial survey resulted in the detection of tanoak mortality and the positive identification of *P. ramorum* at five sites on the south-west coast of OR near the town of Brookings (Curry County), just north of the CA border (Goheen *et al*. 2002). Aerial photos of the area indicate that the pathogen was present at one of the sites since 1997 or 1998 (A. Kanaskie, pers. comm.).

Since autumn of 2001, OR state and federal agencies have been attempting to eradicate *P. ramorum* from infested sites in OR by cutting and burning all infected host plants as well as an adjacent buffer zone (Fig. 2). The forested area in OR under quarantine by the OR Department of Agriculture (ODA) and USDA APHIS was 28 km^2 (11 mi^2) in 2005. This area increased to ~56 km^2 (22 mi^2) in early 2006, and to 67 km^2 (26 mi^2) in 2007. In OR, eradication is mandatory and it is carried out by the landowner. Reimbursement is primarily via federal funds administered by the State Department of Agriculture. Through March 2007, US$1.5 million has been distributed for treatments, with additional costs to monitor the area and manage the program (Kanaskie *et al*. in press).

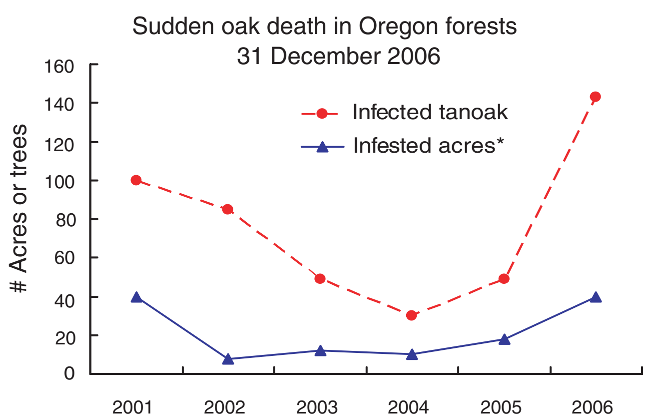

Fig. 2. Sudden oak death trends in Curry County, Oregon, United States. The pathogen is under eradication in Oregon and detected infections are destroyed by removal and burning. Credit: Alan Kanaskie, OR Department of Forestry.

From 2001 through 2006, *P. ramorum* has been detected at 55 nursery sites out of 6067 surveyed in OR at a cost of US$3 178 402 (70% federal funds provided by the USDA). To comply with the quarantine rules in 2007, the ODA must inspect over 1450 nurseries. Nurseries with high-risk plant species, such as *Camellia*, *Rhododendron*, *Viburnum*, *Pieris*, and *Kalmia*, are inspected three times per year (N. Osterbauer, ODA, pers. comm.).

California wildlands and nurseries

California nurseries

Counties where sudden oak death is not known to occur in forests rely on quarantines and best management practices to prevent introduction. Currently in CA, nurseries outside of the quarantine area with high-risk plant species (*Camellia*, *Rhododendron*, *Viburnum*, *Pieris* and *Kalmia*) are inspected three times per year. To comply with the state and federal quarantines in CA, 856 nurseries are inspected annually. From 2001 to 2006, 110 nurseries have been found positive for *P. ramorum* throughout CA. From 1 July 2002 to 30 June 2007, the USDA cooperative agreements with the CDFA have totalled ~US$25 million (K. Kosta, CDFA, pers. comm.).

Wildland management

Humboldt County is the northern-most infested area in CA, because eradication is not feasible, efforts are being made to slow the northward spread of *P. ramorum* in coast redwood (*S. sempervirens*) forests. An isolated infestation of *P. ramorum* in an ~518 ha (2 mi^2) area of redwood forests near the town of Redway, a residential setting in northern CA, was confirmed in July 2002. The area was treated in February 2004 by removing infested tanoaks (Valachovic *et al*. 2006). Additional areas of tanoak mortality in riparian forest settings near Redway and nearby Garberville were confirmed later in 2004. With clear-cutting not an option due to adverse environmental impacts and the residential setting, removal of foliar hosts, such as CA bay laurel was carried out. Experimental silvicultural control projects on more than 48.6 ha (120 acres) were implemented in 2006. The treatments included CA bay laurel and tanoak removal in combination with pile and broadcast burning. Despite suppression efforts, the pathogen has spread to over 1619 ha (4000 acres) in Humboldt County as a result of favourable weather conditions in 2005 and 2006 (Y. Valachovic and C. Lee, pers. comm.).

In 2007, the Pacific Lumber Co. received USDA Forest Service, Pacific Southwest Region funding to create a barrier zone to prevent northward spread. A swath of tanoaks 3.2 km (2 mi) wide by several kilometres long is being treated with herbicides near the Van Duzen River in an effort to try and halt the northward spread of the pathogen. The barrier zone is being created ~80 km (50 mi) north of the infested area in Redway/Garberville.

In addition to suppression efforts in Humboldt County, individual home owners, are attempting to save high-value trees by applying AGRI-FOS to prevent infection. The treatments are coupled with removal of CA bay laurel trees adjacent to oak trees to reduce inoculum levels. For a more complete description of treatments and recommendations, see the Best Management Practices posted at the CA Oak Mortality Task Force website http://nature.berkeley.edu/comtf/html/best_management_practices.html (accessed 15 November 2007).

Hazard tree removal and management programs, to prevent damage from tree failure or fire are also implemented in many of the infested CA counties.

Washington nurseries

While *P. ramorum* has never been found in WA's wildlands, all nurseries in the state that have host plants on site and export interstate are regulated for the pathogen, resulting in 290 annual nursery inspections. From 2001 to 2006 there have been 38 positive detections, with 27 of the 38 positive finds made at retail nurseries. Retail nurseries are not included in the regulations. They are only inspected due to trace-back investigations or other circumstances (N. Dart, WA University Extension, pers. comm.).

Impact on nurseries

The impacts of *P. ramorum* on nurseries have been difficult to quantify. The Canadian government in the '*Phytophthora ramorum* compensation regulations' (2007) states 'Sudden oak death (*P. ramorum*) has caused great economic hardship for nursery and landscape businesses in those regions where it has become established. For example, in 2001, Canada closed its markets to most plant crops from the states of OR and CA. Without reopened market access, OR nurseries alone faced losses in sales to Canada of US$15–20 million'.

There are substantial impacts to nurseries that are found positive for the pathogen. Dart and Chastagner (2007) estimated the number and retail value of plants destroyed in WA nurseries due to *P. ramorum* quarantine efforts between 2004 and 2005. During this period, 17 266 containerised nursery plants were destroyed at 32 nurseries, worth an estimated US$423 043. The mean loss per nursery was estimated at $11 188 in 2004, and $11 798 in 2005. Other US states do not record this information, so comparable statistics are not available.

In addition to the dollar value of the destroyed plants, nurseries also incur the cost of plant destruction. Other unquantified impacts include: loss of customers due to a positive find of *P. ramorum* (lost future sales); fumigation, paving, or other rehabilitation costs; and costs to implement best management practices, such as additional sanitation measures or reduced reuse of materials. An extension horticulturist explained that 'the reality of the situation is the value of the plant material that is destroyed under direction of APHIS only represents a very small percent of the cost nurseries have faced. In speaking to several nurseries, some report destroying thousands of plants before ever being ordered to do so by APHIS in an attempt to minimise potential mitigation costs and escape additional inspections'. The risk and uncertainty created by *P. ramorum* regulation has also caused growers to abandon profitable products (N. Dart, pers. comm.).

Canada has set aside more than US$24 million in *P. ramorum* compensation funds for wholesale and retail nurseries as well as individuals impacted by pathogen eradication efforts (Anon. 2007). Conversely, the US government has not provided compensation to growers.

Suslow (2006) provided an overview of economic impacts and challenges for the nursery industry listing needed improvements in: communications between nurseries, regulators and forestry officials; utilisation of Universal Product Codes to determine product origin; validation of diagnostic tests and more accredited laboratories.

Biosecurity and other issues raised by *P. ramorum* and other new *Phytophthora* spp.

Regulating a newly discovered organism such as *P. ramorum*, is challenging at best. As investigations provide new information, it requires continual updating of host lists, treatments, inspection procedures and other aspects of the quarantine program. The following recent research and monitoring findings pose challenges to regulation and management of *Phytophthora* spp.

Detection of *P. ramorum* in watercourses adjacent to infested nurseries

The detection of *P. ramorum* in watercourses adjacent to infested nurseries is a current biosecurity threat within the US. The first such detection (2006) involved a seasonal stream adjacent to an infested ornamental nursery in WA (COMTF 2006). As part of a national survey of watercourses in the US, Oak *et al*. (2007) reported a repeat detection in that stream. In 2007 thus far there have been four *P. ramorum* positive streams associated with nursery detections outside the *P. ramorum* infested area: two in WA, one in Mississippi and one in CA (Humboldt County). Both the North American (NA1 mating type A2) and European (EU1 mating type A1) strains of the pathogen have been detected in CA (Norton Creek, Humboldt County) (COMTF 2007*b*). The EU strain is not known to be present in wildlands in CA (N. Grunwald, Agricultural Research Service, pers. comm.). Water is not regulated and water-flowing outside of nurseries is not typically of concern to agricultural officials. There is no protocol to follow when *P. ramorum* is found in a river. The likelihood of a contaminated river serving as a pathway for pathogen establishment on vegetation or soil has not been quantified, but can be hypothesised via flooding exposing riparian plants to inoculum.

Sporulation with inconspicuous or no visual symptoms

Sporulation of *P. ramorum* and *P. kernoviae* on asymptomatic foliage was observed by Denman *et al*. (in press) during the evaluation of field trials established to assess inoculum density and natural infection in the UK. Naturally infected, asymptomatic leaves supported sporulation of both pathogens, with 63% of asymptomatic rhododendron leaves yielding *P. kernoviae* and 31% found to have *P. ramorum*.

Production of *P. ramorum* sporangia on asymptomatic leaves was also observed during a laboratory evaluation in Anna Maria, Italy Vettraino *et al*. (2007) of the susceptibility of

65 coniferous and broad-leaved shrubs and trees native to the Mediterranean basin. In this study, another biosecurity challenge was noted: an inverse relationship between lesion size and sporulation level. The plants with the smallest leaf spots produced the highest amounts of inoculum. Based on this finding, the infections hardest to detect during inspections are the most infectious. Linderman and Davis (2007) observed the same plant response while testing susceptibility of *Camellia*. He found a wide range of susceptibility among cultivars, but a lack of correlation between susceptibility (lesion size) and potential to produce sporangia that might spread the pathogen within a nursery. He concludes, 'These results indicate that on some cultivars the pathogen might produce small or inconspicuous lesions, yet still produce copious numbers of sporangia that could spread the disease, both within the nursery and from nursery to nursery'.

Survival and infection from infested potting mix

Parke and Lewis (2007) demonstrated *P. ramorum* infection occurring via roots of Pacific rhododendron (*R. macrophyllum*) plants transplanted into a potting medium artificially infested with the pathogen. Dieback occurred in the leaves and stem but the infected roots were asymptomatic. The authors conclude that this 'demonstrates the need to monitor potting media for presence of the pathogen to prevent spread of *P. ramorum* on nursery stock'.

The greenhouse and nursery soilborne phase of *P. ramorum* has also been demonstrated by Shishkoff (2007). Colonies of *P. ramorum* could be recovered from moist potting mix or sand for many months, whether buried as infected plant leaf tissue or as mycelium bearing chlamydospores. *P. ramorum* could also be recovered from the internal portions of *Rhododendron*, *Camellia*, and other host plant root tissue after sporangial root drenches. When chlamydospores were placed near roots, they were found to germinate, which led to the formation of sporangia and infection in nearby roots.

Using *P. ramorum* as a case study of a regulated ornamental pathogen, Daughtrey and Benson (2005) noted the potential for pathogen transport via soilborne chlamydospores. They state that the incomplete understanding of the biology and epidemiology of *P. ramorum* on nursery crops could represent weak links in the regulatory plan and cite that the US regulatory program lacks measures to prevent movement of soilborne inoculum on asymptomatic plants.

Increased detection of new *Phytophthora* spp.

Phytophthora spp. are well documented as frequently occurring, damaging pathogens in ornamental nurseries (Ferguson and Jeffers 1999; Osterbauer *et al*. 2004; Jung *et al*. 2007; Snover-Clift *et al*. 2007) but *P. ramorum* has refocussed attention on foliar nursery plant infections. Yakabe *et al*. (2007) recovered 14 *Phytophthora* spp. causing foliar infections on nursery plants during an evaluation of *Phytophthora* spp. detected during mandated regulatory nursery surveys for *P. ramorum.* Several of the species detected, such as *P. foliorum* (Donahoo *et al*. 2006), *P. pseudosyringae* (Jung *et al*. 2003), and *P. nemorosa* (Hansen *et al*. 2003) are newly discovered *Phytophthora* spp. Other species such as *P. hibernalis* (Blomquist *et al*. 2005), and *P. tropicalis* (Hong *et al*. 2006) have only recently been detected on ornamental plants.

Similar surveys in Minnesota nurseries detected eight *Phytophthora* spp. including, *P. hedraiandra.* This was the first time *P. hedraiandra* had been detected in the US, and the first time it had been detected on rhododendron. Previously *P. hedraiandra* had only been recovered from *Viburnum* in the Netherlands (Schwingle *et al*. 2006, 2007). Also detected were the previously identified but undescribed *Phytophthora* taxon Pgchlamydo and two additional isolates that did not match known species.

Over the past few years, several of the *Phytophthora* spp. detected in ornamental nurseries, such as *P. ramorum*, *P. kernoviae*, *P. pseudosyringae*, and *P. nemorosa*, have been isolated from dying forest trees (Rizzo *et al*. 2002; Hansen *et al*. 2003; Brasier *et al*. 2005). The movement of *Phytophthora* on nursery stock is apparent and the potential for inadvertent introduction of *Phytophthora* spp. capable of killing trees in susceptible forest environments is increasing as more and more people landscape their homes in new developments in urban/wildland interface environments.

As our understanding of *Phytophthora* advances and technology improves, the rate at which new *Phytophthora* spp. are discovered continues to increase. Clive Braiser observed that 54 *Phytophthora* spp. were known worldwide in 1996 as reported in Erwin and Ribeiro (1996). He reports the discovery of at least an additional 50 *Phytophthora* spp. in the past 10 years or so, with the majority of the new *Phytophthora* spp. associated with tree mortality (C. Brasier, pers. comm.). Many of the new species such as *P. ramorum* have wide host ranges, including many plants common in the nursery trade.

The origin of many of these new *Phytophthora* spp. is not known and is difficult to determine. Ramsfield *et al*. (2007) report that *P. kernoviae*, first described in 2005, was speculated to have been introduced to the UK from Asia or South America. However, recent DNA sequence studies of *Phytophthora* spp. curated in New Zealand culture collections revealed an isolate of *P. kernoviae* recovered in 2002 from diseased custard apple (*Annona cherimola*) orchards. Further studies have shown that *P. kernoviae* is present in soils in both indigenous and exotic forests in several regions of the North Island, New Zealand, and historical data indicates that it was first recorded in New Zealand (as *Phytophthora* sp.) in the 1950s. These findings raise the possibility that *P. kernoviae* is resident in the South Pacific. However, currently only a hypothesis, the pathway of *Phytophthora* to the UK is still unknown. The worldwide distribution of *Phytophthora* spp. is not fully understood, nor are the pathways or conditions that lead to new forest disease outbreaks.

Final thoughts

As presented in this overview, the research, regulation, and management of *P. ramorum* has raised many challenging and unanswered biosecurity questions:

(1) What is the relationship between nursery diseases and forest diseases?
(2) How should a country respond when they learn a resident *Phytophthora* is causing a problem on another continent?

(3) How can we recognise the next important *Phytophthora* sp. before it has killed too many plants and is unstoppable?
(4) How can we regulate to protect against *Phytophthora* spp.? Can we effectively regulate on a species by species basis?
(5) How can we regulate for symptomless infection?
(6) How can we eradicate, suppress or manage wildland *Phytophthora* spp.?
(7) Are waterways the primary habitat for *Phytophthora*? What is the ecological role of *Phytophthora* spp. in water courses? How can water be regulated?
(8) How can we engage scientists, policy makers, politicians, and the public to raise awareness and funding to address these *Phytophthora* problems?

The chronology of sudden oak death and *P. ramorum* demonstrates the vulnerabilities of forests; agriculture, forestry, and horticulture industries, as well as associated land management, regulatory, and scientific agencies. The outlined challenges need to serve as a rallying cry for regulatory agencies, plant pathologists, and horticulturists, and other affected entities worldwide to work together to revise systems aimed at preventing the spread of *Phytophthora* spp. and other plant and forest pathogens.

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