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SHORT COMMUNICATION

Update on the 35-year expansion of the invasive root pathogen, *Phytophthora lateralis*, across a landscape of Port Orford cedar (*Chamaecyparis lawsoniana*)

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Summary

Port Orford cedar (*Chamaecyparis lawsoniana*) is endemic to northern California and southwestern Oregon and is considered a foundation species that plays critical roles in riparian areas and on nutrient-poor soils. Since 1952, a non-native, pathogenic oomycete (*Phytophthora lateralis*) has been spreading throughout the range of the cedar. Most spread occurs by vehicles carrying infested soil along gravel roads primarily used for timber harvest. In a previous study conducted in 1998 and 1999, Port Orford cedar and *P. lateralis* were censused in a 37-km^2 study area and dendrochronology was used to reconstruct the history of pathogen invasion. That work, which represents the only detailed analysis of spread rates for *P. lateralis*, showed that the first successful invasion into the study area took place in 1977 and that 43% of the susceptible host sites (stream crossings) were infested by 1999. In the work presented here, all sites that were uninfested in 1999 were re-censused in 2012, extending the historical reconstruction of *P. lateralis* spread to 35 years. Two new infestations were initiated between 1999 and 2012, suggesting that the rate of spread of *P. lateralis* has slowed greatly. Between 1980 and 1989, the average number of new site infestations was 1.8 infestations per year, while between 1990 and 1999 the average was 0.4 infestations per year and between 2000 and 2009 the average was 0.2 infestations per year. Several potential explanations for the reduced number of new infestations are discussed.

1 Introduction

Port Orford cedar (*Chamaecyparis lawsoniana*) is a large tree restricted to relatively moist areas in southwestern Oregon and northern California (USA; Fig. 1). Considered a foundation species, it plays important roles in stabilizing riparian areas and increasing calcium availability on nutrient-poor soils, especially those derived from ultramafic parent rock (Hansen et al. 2000). In 1952, a root pathogen, *Phytophthora lateralis*, was accidentally introduced into the native range of Port Orford cedar (Hansen et al. 2000). The pathogen is fatal for almost all infected cedars and has since spread into most regions within the cedar's range (Hansen et al. 2000). The pathogen has significant impacts on cedar populations: up to 44% mortality has been found in some cedar populations and other sites are likely to show higher rates of mortality (Kauffman and Jules 2006; Jules et al. 2014). Although some maps of the distribution of *P. lateralis* have been produced and periodically updated, they are coarse in resolution and frequently missing infested sites due to the difficulty in conducting careful surveys (Jules et al. 2002).

Spread of the pathogen occurs over long distances by vehicles carrying infested soil, primarily along gravel roads that serve areas used for timber harvest and other commercial and recreational activities such as mushroom gathering and hunting (Hansen et al. 2000). Because Port Orford cedar is restricted to moist areas, new infestations often begin when infested soil is accidentally deposited alongside a road near a stream crossing (Jules et al. 2002). Once the roots of a nearby cedar have been infected, the pathogen produces zoospores that can be transported downstream to infect other cedars along the stream. Thus, infestations of streams are often the result of single events that are independent of other infestations, and they result in whole stream courses becoming infested. Movement of the pathogen occurs secondarily over short distances via foot traffic (e.g., ungulates and humans moving infested soil; Hansen et al. 2000; Jules et al. 2002). The risk of any one site (e.g., stream) becoming infested has been related to the amount of host found alongside the road and the amount of vehicle traffic crossing the stream (Jules et al. 2002).

Port Orford cedar presents a unique opportunity for the study of invasive pathogens because the date of infection can be determined for dead cedar even decades after mortality. The wood of Port Orford cedar is remarkably decay-resistant, such that a dead cedar may remain standing with intact wood and bark for many decades after death (Carroll and Jules 2005). Using increment cores extracted from the dead trees, the dendrochronological technique of cross-dating can be used to determine the year of infection. In a previous study, Jules et al. (2002) examined a study area where Port Orford cedar is highly restricted to riparian areas such that its distribution largely reflects the network of streams. In their study, Jules et al. (2002) censused all cedar-bearing streams and used cross-dating to reconstruct the history of disease. That work, conducted in 1998 and 1999, showed a 19-year invasion that had begun in 1977 with the infestation of one stream and spread to 46% of the total length of streams in the area. The work presented here is a second census of the study area conducted in 2012. The goal of the present study was to detect any new infested sites and use cross-dating to determine the year of infestation. The study extends the invasion reconstruction to 35 years and represents the most detailed account of *P. lateralis* spread to date.

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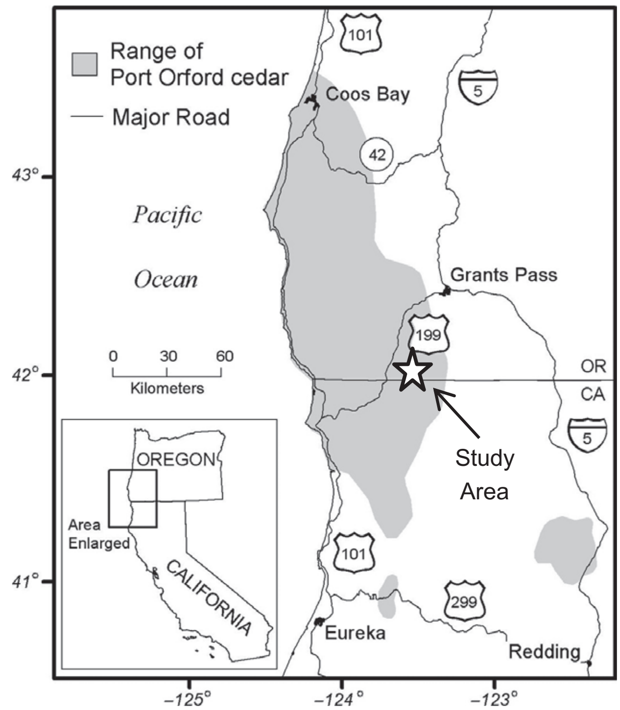

Fig. 1. The range of Port Orford cedar (*Chamaecyparis lawsoniana*) and the location of the study area (open star). The study area is a 37-km^2 area that straddles the California–Oregon border and is entirely within the boundaries of the Rogue-Siskiyou National Forest.

2 Material and methods

The study area encompasses 37 km^2 in the Siskiyou Mountains of southwestern Oregon and northern California (Fig. 1) and is entirely within the boundaries of the Rogue-Siskiyou National Forest. Vegetation in the study area is dominated by mixed conifer forest comprised of Douglas fir (*Pseudotsuga menziesii)*, incense cedar (*Calocedrus decurrens*), tanoak (*Notholithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*). The most common resource management activity has been timber harvesting; by the time of the previous census in 1998 and 1999 by Jules et al. (2002), 35% of the area had been logged (see Jules et al. 2002). Within the study area, Port Orford cedar is mostly restricted to wet areas near streams, seeps and other mesic sites, and it is the dominant tree in riparian areas. There are 63 km of streams occupied by the cedar within the study area, and 93 km of roads that cross the streams at 86 locations. The 86 stream crossings are the locations where *P. lateralis* can be accidentally introduced into the area by passing vehicles carrying spore-laden soil (Jules et al. 2002). At the time of the previous census, 37 of the 86 stream crossings were infested with *P. lateralis*.

In September 2012, all 49 stream crossings that were occupied by Port Orford cedar and uninfested in 1999 were recensused. Each site was searched at least 200 m downstream of crossings for the presence of *P. lateralis* infection of cedars using visual symptoms of leaf discoloration or mortality. The study of Jules et al. (2002) found that 96% of infestations initiated within 100 m of crossings (mean distance = 25 m). For newly infested sites, 2–3 increment cores were collected from six symptomatic cedars that were near the origin of the infestation. Cores were later fixed onto wood mounts and progressively sanded to 600 grit, and ring widths were measured to 0.001 mm precision using a WinDendro image analysis. Cross-dating of cores was accomplished by aligning ring-width patterns visually and confirmed using the program COFECHA to statistically compare ring-width series from dead trees to a master ring-width chronology (see Carroll and Jules 2005 for detailed methods). The year of infestation (which may predate death by several years) was estimated by noting the beginning of growth reduction of rings as a result of massive fine root losses caused by *P. lateralis* (Jules et al. 2002; Kauffman and Jules 2006).

3 Results and Discussion

Of the 49 sites not infested at the time of the previous census by Jules et al. (2002), only two became infested between 1999 and 2012. At these two sites, numerous dead and dying trees were present and all six trees sampled with increment borers at the top of the infestation showed signs of chlorosis (either overall yellowing or overall browning) or were dead. Cross-dating was difficult due to the young age of the infected trees, with an average of 32 years per core. Accordingly, five of six trees were cross-dated in one site, while only two of six trees were cross-dated at the second site. Successful cross-dating of the five cores suggest that a new infestation started in 2003, while the best estimate that can be made for the infestation at the second site is 2006. Regardless of the precision of the estimates of infestation year, the recent rate of

new infections has been markedly lower than the rate observed at the start of the invasion by Jules et al. (2002; Fig. 2). In the first 10 years of the invasion (1977–1986), *P. lateralis* infested an average of 1.6 sites per year; in the second 10 years (1987–1996), it infested an average of 0.5 sites per year; and in the final 10 years (2003–2012), it infested 0.2 sites per year.

There are several possible reasons for the observed reduction in new infestations, and each is discussed below. First, if most of the highly susceptible stream crossings had already been infested, then the pool of 49 uninfested sites in 1999 may have been comprised mainly of low-risk sites. For the cedar–*Phytophthora* system, previous work has shown that the risk of infestation at a stream crossing increases with the number of host trees near the crossing and the amount of water flowing under the crossing (Jules et al. 2002). For example, host abundance at stream crossings in the study area had previously been measured as the number of cedar found within 15 m of the road (Jules et al. 2002), and sites that had been infested by 1999 had, on average, 18.5 cedars ($\pm$1.0 SD = 16.3), while uninfested sites had 6.0 cedars ($\pm$1.0 SD = 11.1). Thus, if most of the uninfested sites had few cedars and relatively dry streams, then their risk may have been low. However, sites that were uninfested in 1999 still included a large number of high-risk sites. For instance, in 1999, there were five sites with more than 18.5 cedars and nine sites with more than 10 cedars. The two newly infested sites were of low and moderate host density; one site had a host density of 12 cedars and the other had no cedars (e.g., there were no cedars within 15 m of the road crossing). In addition, there is no indication that host density had changed markedly between the two censuses: mechanical removal of cedars along roads has been used in many parts of the cedar's range in an attempt to reduce infestation risk (i.e., 'sanitation logging'); however, this technique has only been used in one location in the study area and has subsequently been naturally reseeded with many Port Orford cedars (E. Jules, *personal observation*). Similarly, there remained a sizeable pool of uninfested sites with high flow accumulation and thus high risk (Jules et al. 2002). Although our sample size is too small for a formal statistical analysis, there is little support for reduced site risk driving the reduction in new infestations.

A second potential explanation of the small number of new infestations is a decline in vehicle traffic since the earlier census by Jules et al. (2002), which would reduce 'propagule pressure' at all sites. This reduction in propagule pressure would be especially true if there had been a reduction in heavy vehicle traffic, such as that associated with timber harvesting, because heavy equipment moves large amounts of infested soil. The amount of traffic related to timber harvesting has declined markedly since the initial decade of the *P. lateralis* invasion in the study area. Because of court orders in 1989 and 1991 related to the management of the Northern Spotted Owl (*Strix occidentalis caurina*), timber harvest in National Forests within the Pacific Northwest declined sharply (Fig. 2). With the adoption of the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994), Spotted Owl-related injunctions ended, although timber harvests never reached their historically high rates again. As an example, estimated timber harvest levels (in hectares harvested) are shown for the study area (Fig. 2). Harvesting remained steady through 1990, then dropped markedly thereafter. A reduction in vehicle traffic can also be caused by road closures. In the study area, no roads have been decommissioned during the period of study; however, two small segments of road have been closed due to road failures, and these rendered two potential infestation sites accessible only by all-terrain vehicles. Although there is no means to directly test this conjecture in our study, a reduction in vehicular traffic cannot be rejected as an explanation of the reduced infestation rate given the data presented here.

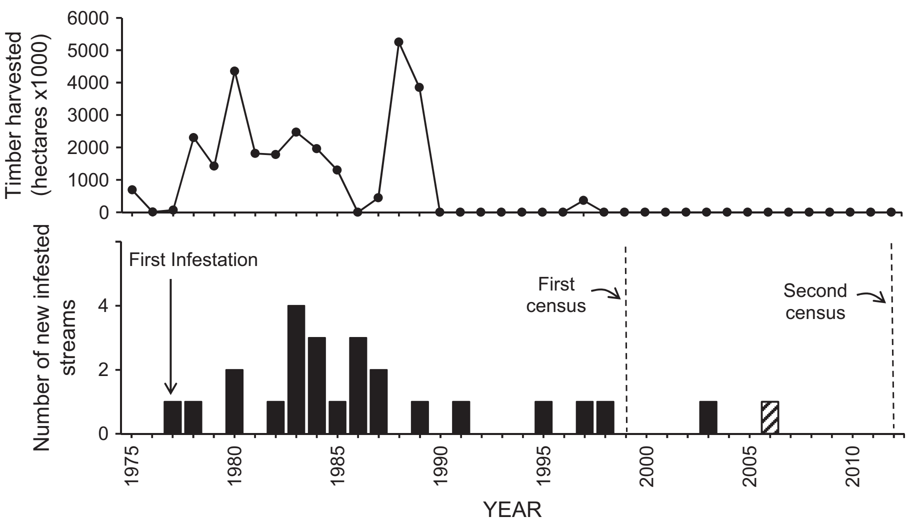

Fig. 2. The number of new site infestations (streams) within the study area between 1977 and 2012 (bottom panel). New infestations are streams occupied by Port Orford cedar (*Chamaecyparis lawsoniana*) that are crossed by roads and have been infected by the oomycete *Phytophthora lateralis*, generally by vehicles accidentally dropping spore-infested soil at stream crossings. The hatched bar in 2006 indicates that the date of infestation shown is an estimate and lacks precision. Also shown is an estimate of the amount of timber harvested (hectares harvested) each year in the study area.

Third, management of the study area is conducted almost entirely by the US Forest Service, which is mandated to assess risk to Port Orford cedar and to implement mitigation measures to protect the cedar against new infestations. The agency is guided by an Environmental Impact Statement and Record of Decision aimed specifically at managing for the protection of Port Orford cedar (USDA Forest Service and USDI Bureau of Land Management 2004). Attempts to mitigate risk of new infestations can be accomplished through various techniques, including scheduling timber harvesting projects during the dry season, washing equipment of potentially infested soils, minimizing ground-based logging systems (e.g., instead opt for cable or helicopter systems) and sanitation logging (see above). The degree to which these strategies have been employed in the study area is unknown and would be difficult to evaluate. Interestingly, one of the two newly infested sites occurred within the boundaries of a unit in which timber harvesting had occurred within the past few years. Nonetheless, the implementation of mitigation strategies offers yet another potential explanation for the observed reduction in new infestations by *P. lateralis*.

Finally, a fourth explanation of the reduction in new infestations is a change in precipitation and/or flooding events. Reduced precipitation could have resulted in fewer spores being successfully transported from infested to uninfested sites as *P. lateralis* requires moist conditions for survival and long-distance movement (Hansen et al. 2000). Such a difference in precipitation would probably need to be significantly different between the two census periods to explain differences in infestation rates. Both mean annual and mean monthly flow rates at a downstream USGS gauging station (Illinois River near Kerby, Oregon) were assessed, and no differences between the two census periods were found ($t = 0.327$, d.f. = 34, $P = 0.745$). In addition, the final ten years of the invasion were not different than the first 10 years or the second 10 years in flow rates ($F = 1.237$, d.f. = 2, $P = 0.306$). There is no indication that changes in flow rates can account for the reduction in new infestations.

It is unclear whether the study area is representative of the whole range of Port Orford cedar, although personal observation by the first author suggests that new infestations have slowed throughout the range. Important long-distance movements of the disease into relatively isolated areas continue to be noted however. For instance, new infestations into wilderness area (both the Kalmiopsis and Siskiyou Wilderness Areas) and into the southern extent of the cedar's range (Willow Creek) have occurred in the last decade. This study discussed several plausible reasons for why the spread of *P. lateralis* has slowed in the study area: a general attrition of sites with the highest infestation risk; a reduction in commercial vehicle traffic associated with timber harvesting; and a change in precipitation. Given the continued presence of high-risk sites and steady precipitation in the study area, there is only support, albeit limited, for an explanation which includes the reduction in vehicle traffic.

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