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Susceptibility to the rare *Phytophthora tentaculata* and to the widespread *Phytophthora cactorum* is consistent with host ecology and history

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Abstract

We evaluated the susceptibility of three California endemic plant species *Heteromeles arbutifolia*, *Platanus racemosa* and *Quercus agrifolia* to the two congeneric soilborne pathogen species: *Phytophthora tentaculata* and *Phytophthora cactorum*. These pathogens were recently introduced in ecosystems east of the San Francisco Bay, where the three plant species above are dominant. *Phytophthora cactorum* has a worldwide distribution inclusive of California, and a broad host range. *Phytophthora tentaculata*, in contrast, is suspected to be a "new" exotic to California and has been described on relatively few hosts. By separately challenging the roots and the stems of the three plant species above, we show that: (a) Both were equally pathogenic, but the type of disease differed based on host; (b) disease was consistent with host ecology and with previous disease reports, even if caused by different *Phytophthora* spp. and; (c) there were intraspecific differences in virulence. This study provides the following significant information regarding the management and early modelling of polyphagous soilborne *Phytophthoras*: (a) Endemic species can be as problematic as recently introduced exotics. (b) Multiple introductions should be avoided due to varying virulence levels among genotypes. (c) Riparian species like *P. racemosa* may develop disease tolerance in their root systems, but remain susceptible in their aerial portions, and thus, diseases could be facilitated by flooding or splash of infectious structures of soilborne pathogens onto aerial plant portions.

KEYWORDS

California sycamore, coast live oak, host ecology, pathogenicity testing, soilborne pathogens, toyon

1 | INTRODUCTION

Phytophthora is a genus of plant pathogenic water moulds belonging to the Kingdom Stramenopila. The genus contains over 100 described species (Kroon, Brouwer, de Cock, & Govers, 2012), many distributed worldwide (Erwin & Ribeiro, 1996) and often reported from nurseries (Bienapfl & Balci, 2013; Parke, Knaus, Fieland, Lewis, & Grünwald, 2014). Additionally, many such species are currently prominent in lists of emerging threats to natural ecosystems around the world (Brasier, 2008; von Broembsen, 1989; Goss, Larsen, Chastagner, Givens, & Grünwald, 2009; Hansen, 2008, 2015; Rizzo, Garbelotto, Davidson, Slaughter, & Koike, 2002). *Phytophthora tentaculata*, for instance, has been listed in the top five *Phytophthora* species of concern to the United States (APHIS 2010; Rooney-Latham & Blomquist, 2014).

The potential for the introduction of plant pathogens into restored wildlands through infected nursery plant stock is high (Jung et al., 2015), but has not been thoroughly investigated, especially in North America. In a recent evaluation of native plant nurseries and restored wildlands in California, it has been shown that *P. tentaculata*

Kröber & Marwitz and *P. cactorum* (Lebert & Cohn) J. Schröt. may have been moved from nurseries into restoration sites via infected plant stock (Rooney-Latham, Blomquist, Swiecki, Bernhardt, & Frankel, 2015). Evaluation for *Phytophthora* species at sites prior to restoration efforts would help to understand species distributions (Sims, Sutton, Reeser, & Hansen, 2015). These sorts of efforts were not used herein, but instead this study was part of a reaction after the restorations took place.

Phytophthora tentaculata is considered exotic to the United States, while *P. cactorum* has a worldwide distribution inclusive of the West Coast of North America, but it has never been reported from drier grassland-savanna habitats, such as those found in the eastern portion of the San Francisco Bay Area.

These two *Phytophthora* species have now been found to be associated with outplanted nursery-grown toyon (*Heteromeles arbutifolia* (Lindl.) M. Roem.) and orange bush monkey flower (*Diplacus auarantiacus* (Curtis) Jeps.). Two additional plant species, California sycamore (*Platanus racemosa* Nutt.) and coast live oak (*Quercus agrifolia* Née), are endemic and prominent in infested restoration sites. Thus, the release of these two pathogens currently threatens all four plant species. The study described herein emphasized California sycamore because it was the major remnant species in the savanna restoration. While the susceptibility of orange bush monkey flower to *P. tentaculata* has been recently demonstrated (Rooney-Latham & Blomquist, 2014), this study examined the susceptibility of toyon, California sycamore and coast live oak which still needed to be evaluated.

Exotic microbial pathogens can have unpredictable ecological impacts on natural ecosystems (Cave, Randall-Schadel, & Redlin, 2008), and their effects may be compounded by high levels of virulence on native hosts due to lack of coevolution between hosts and pathogens (Garbelotto, Rocca, Osmundson, di Lonardo, & Danti, 2015; Leonard & Czochor, 1980; Loo, 2008). It is believed that *P. tentaculata* may be exotic to California because, prior to 2012 (Rooney-Latham et al., 2015), this species had been reported exclusively from outside the United States. Countries it has been reported from, including more recent reports, are Germany, Spain, China, Italy, Japan, the Netherlands and the United Kingdom (Beal, Waghorn, Scrace, & Henricot, 2018; Kröber & Marwitz, 1993; Martini et al., 2009; Moralejo, Puig, & Man in't Veld, 2004; Rahman et al., 2014; Wang, Zhao, & Qi, 2014; Yang, Tyler, & Hong, 2017). The known host list of *P. tentaculata* from these countries and the United States is relatively limited, around 20 but probably growing. By contrast, *P. cactorum* is known to parasitize over 200 plant species around the world, California included (Erwin & Ribeiro, 1996). Its broad host range increases the chances that its accidental release into wildlands may result in a successful invasion of new ecosystems. *Phytophthora cactorum* has primarily been reported as a problem in commercial nurseries and urban plantings in the US West Coast (Sinclair & Lyon, 2005), where native plant species such as madrone (*Arbutus* species), dogwood (*Cornus* species) and toyon have been used as planting stock (Elliott, 1999; Keim, Mock, & Guenther, 1976; Stuntz & Seliskar, 1943). It has now also been described as the most common species associated with toyon in planted restoration sites in Santa Clara County (Bourret et al., 2018), suggesting it is now a part of planted ecosystems on this host.

In this study, we tested the effect of inoculation and possibly drying stress by inoculating *P. tentaculata* and *P. cactorum* on California sycamore, coast live oak and toyon, and then allowing plants to dry at the end of experiments. All three studied plant species are major components of various California ecosystems with overlapping distributions. Based on 1,440 observed accounts (Jepson Flora Project, 2018), toyon occurs commonly in chaparral plant communities in canyons and on slopes. It occurs throughout much of the western portion of the California floristic province from the North Coast and Klamath Range south to the San Jacinto Mountains, in its central distribution as far east as the High Sierras. Based on 995 accounts of coast live oak (Jepson Flora Project, 2018), it occurs mainly in oak woodland communities and in mixed evergreen forests from the outer North Coast Ranges southward, throughout the San Francisco Bay Area including in the eastside oak savannas. Coast live oak associates with California sycamore (Steinberg, 2002) just outside riparian areas and also occurs in a shrubby form in chaparral communities where toyon is found. Observed accounts (886; Jepson Flora Project, 2018) of California sycamore suggest it occurs as a component of many different plant communities in foothills woodlands, chaparral and riparian ones mainly from the Cascade Range foothills across the Sacramento Valley, in riparian areas of oak savanna sites, south-west to the central coast and most common in the southern portions of California. Hence, this work is an essential prerequisite to correctly predict future impacts of *Phytophthora* species in many regions of California. In addition, we used these new pathosystems to test four primary hypotheses motivated by three sets of criteria. The first set implied that the type of disease (above ground vs. root disease) caused by different soilborne *Phytophthora* species should be predictable based on previous reports, even if caused by different but congeneric *Phytophthora* species. The second set implied that the differing ecology of plant hosts (riparian California sycamore vs. non-riparian coast live oak and toyon) might have resulted in different exposure histories to *Phytophthora* species or other similar organisms, which could ultimately be responsible for the selection of disease tolerance on plant species or plant populations with a history of exposure. Finally, the third set implied that canopy symptoms in a deciduous riparian tree species (California sycamore) would be measurable in the short term, as opposed to canopy symptoms on drought-tolerant evergreen species.

The four specific hypotheses tested in this study were as follows: (a) Disease would be caused by both *P. tentaculata* and *P. cactorum* on toyon, but symptoms would develop mainly in the root and root collar. (b) Coast live oak would be susceptible to both *P. tentaculata* and *P. cactorum*, and disease would develop both in the roots and stems. (c) California sycamore would be susceptible to both *P. tentaculata* and *P. cactorum*, and the canopy would develop symptoms, but the roots would resist at least

P. cactorum. (d) *P. tentaculata* would be able to cause more severe disease symptoms than *P. cactorum* on each of the tested hosts.

2 | METHODS

Three separate pathogenicity experiments were conducted to test the effects of inoculation of *P. cactorum* and *P. tentaculata* on California sycamore, coast live oak and toyon. Experiments 1 and 2 were designed to provide comparative information on susceptibility of each of the three plant species to each one of the two *Phytophthora* species. Experiments 1 and 3 also examined the possible effects of drying stress on plants. Experiment 3 was designed to study the correlation between canopy symptoms and stem lesions on a single host, but each of the two pathogen species was employed to obtain comparative results.

The first experiment was a root and root collar inoculation of the three plant species with the two *Phytophthora* species, using as inoculum a liquid medium containing zoospores, mycelia and oogonia of each species. The health of roots and root collars was then rated using an ordinal rating scale at the end of a 30-day period. The second was a stem inoculation placing an agar disc colonized with mycelia on the pinprick wounded stems of the three species. Stem cankers were then evaluated following a 14-day incubation period. The third test was similar to test two, but only utilized California sycamore and foliage symptoms were rated as well as canker symptoms. The last test focused on California sycamore because of its importance within a major contaminated restoration as it was the remnant species ecologically and aesthetically valuable due to age (which in some cases likely exceeded 150 years) and size. This test also focused on inoculation with *P. tentaculata* (3 vs. 1 isolate of *P. cactorum*) because it was perceived as the invasive of concern.

2.1 | Plant and pathogen units

2.1.1 | Plant units

Two-year-old plants were used in the three experiments. In each test, 25 plants of each species were used except in Test 2 for which only 15 toyons were available. The toyons were in D40 container type, while coast live oak and California sycamore were in one-gallon containers. They were purchased from California native plant nurseries and were held and screened for pathogens in a University of California lath house for at least 90 days prior to the experiments. Plants were moved into an indoor quarantine-level facility for 7 days before being inoculated following a random design. Before the experiments, each plant was screened for *Phytophthora* by baiting (McIntosh, 1964; Sims, 2014; Sutton, Hansen, Reeser, & Kanaskie, 2009; Themann & Werres, 1998) using a three-bait system. One tablespoon of the potting medium/roots was removed at two different depths from two spots near the outer edge of containers of each plant using a Fisherbrand™ Scoopula™ spatula. Samples within a plant species were combined and baited with leaf and stem pieces from organically grown Oregano (*Origanum vulgare*), organic d'Anjou pear pieces and leaf pieces of *Rhododendron macrophyllum* "Cunningham's White," along with a negative control (water and bait of all three types). In addition, root systems were visually inspected for root necrosis, and plants with any symptoms of necrosis were discarded.

2.1.2 | Isolates

Three isolates of *P. cactorum* and four isolates of *P. tentaculata* were used in the experiments as indicated (Table 1). All isolates were used in Test 1; four isolates, two each of *P. cactorum* and *P. tentaculata* were used in Test 2 (Table 1a); and four isolates one of *P. cactorum* and three of *P. tentaculata* were used in Test 3 (Table 1b).

2.2 | Test 1. Root inoculation

2.2.1 | Plant test conditions

Plants were flooded for 24 hr prior to inoculation and maintained flooded with the inoculum or the mock-inoculum present for an additional 48 hr. Plants were then watered as needed (checking every 1–2 days). The last 10 days of the experiment, no water was applied to simulate dry field conditions.

TABLE 1 Isolate list including collection information, host and pathogen information

Name	Isolate	Collector	County, State	Host	*Phytophthora* species
Pt1	MUAP06098675-4[a,b]	S. Rooney-Latham	Butte, California	*Diplacaus aurantiacus*	*Phytophthora tentaculata*
Pt2	010P06220159-5	S. Rooney-Latham	Alameda, California	*D. aurantiacus*	*P. tentaculata*
Pt3	MUAP06098685-4[a,b]	S. Rooney-Latham	Monterrey, California	*D. aurantiacus*	*P. tentaculata*
Pt4	010P06220151-3-1[b]	S. Rooney-Latham	Alameda, California	*D. aurantiacus*	*P. tentaculata*
Pc1	MP-19[a,b]	P. Hamm	Lewis, Washington	*Pseudotsuga menziesii*	*Phytophthora cactorum*
Pc2	7HET.RH.1	L. Sims	Alameda, California	*Heteromeles arbutifolia*	*P. cactorum*
Pc3	8HET.RH.1[a]	L. Sims	Alameda, California	*H. arbutifolia*	*P. cactorum*

Notes. All isolates were used in Test 1.
[a]Isolates used in test 2. [b]Isolates used in test 3.

TABLE 2 Rating scale used to delineate root symptoms in Test 1

Rating	Description of symptoms
1	Symptomless
2	Small root lesions or small root collar canker, apparent to the naked eye
3	Obvious root disease, at least moderate lesions, plus root collar canker *or* main root beginning to degrade
4	Obvious root disease, more than moderate lesions (=broken/gone), root collar canker *and* main root heavily degraded
5	Girdling canker and main root rotted away
6	Top dead and complete root system rotted away

2.2.2 | Pathogen suspension and zoospore production for treatments

Four isolates of *P. tentaculata* and three of *P. cactorum* were used for root inoculations (Table 1, all isolates). Cultures were grown on a V8 agar, and then six agar discs were removed from 7-day-old colonies and placed in an empty Petri dish; 20 ml of clarified V8 was added and incubated for 7 days at 18°C in the dark. The liquid V8 medium was decanted and replaced with filter sterilized creek water, prepared by filtering through an approximately 2 cm thick Celite® 545 filter and then a Whatman® 2 μM membrane, then 20 ml was poured into each dish. These plates were incubated at 18°C until sporangial production reached a maximum, and then plates were submitted to a cold-ionization shock (20 ml 4–5°C deionized water was placed in each plate) and allowed to come to room temperature ~22°C for 4 hr in order to stimulate zoospore release (Ribeiro, 1978). The approximate number of zoospores was estimated by counting a sample of (40 μl) of the homogenized zoospore liquid with a hemocytometer, loading 10 μl at a time. This was done from the contents of two plates for each of the seven isolates. In addition, every plate was quickly inspected under a dissecting scope to confirm the presence of zoospores and of oospores. All plants were inoculated within 4 hr of zoospore liberation.

2.2.3 | Pathogen inoculation treatment

Inoculation methods were slightly modified from Rooney-Latham and Blomquist (2014). A 40 ml pathogen suspension containing an estimated 1.6×10^5 zoospores was inoculated on each plant, whereby, a small slit was placed at the root collar at the soil line and the pathogen suspension was inoculated over the wound. For plants in 1-gallon pots, the system was draped with polyethylene sheeting from the stem base downward over the edge of the container to help retain moisture. Similarly, for the toyon plants in D-40 pots, the system was covered with Parafilm® M sealing film.

2.2.4 | Severity rating system

Severity was assessed for each plant on the 1–6 ordinal scale outlined (Table 2) following 30 days of incubation. To help keep scores precise, only one person did the scoring. The scoring system used was similar to methods for scoring leaves (Madden, Hughes, & van den Bosch, 2011) but has also been used to evaluate diseased roots (Krause, Madden, & Hoitink, 2001; Madden et al., 2011; Sánchez, Andicoberry, & Trapero, 2005; Sánchez, Caetano, Ferraz, & Trapero, 2002; Serrano, De Vita, Fernández, & Sánchez, 2012). Phytophthora root disease was evaluated for each plant species based on the mean severity rating and the total proportion of plants with an obvious moderate level of visible root disease (severity rating ≥ 3) in a similar way to previous work by Krause et al. (2001). At least a quarter of the root mass contained symptoms at each described level to warrant the rating. Results, as well as summary statistics, are presented in Table 3.

2.2.5 | Reisolation

Segments (3–4 mm long) from inoculated and control roots were plated on Phytophthora selective culture media ½VARP + (V8-based agar amended with 10 ppm pimaricin, 200 ppm ampicillin trihydrate, 10 ppm rifampicin, 15 ppm benomyl and 25 ppm hymexazol

TABLE 3 Root symptom rating summary statistics comparing *Phytophthora tentaculata* and *Phytophthora cactorum* on the three tested plant species in Test 1

Root symptoms				
	Mode of symptoms rating		Maximum rating (No. of plants)	
Host	*P. tentaculata*	*P. cactorum*	*P. tentaculata*	*P. cactorum*
Coast live oak (*Quercus agrifolia*)	3	3	4 (2)	4 (1)
Toyon (*Heteromeles arbutifolia*)	2	3	4 (1)	3 (5)
California sycamore (*Platanus racemosa*)	2	1	2 (7)	2 (2)

[97%]) modified from Sims et al. (2015, VARP+) for reisolation of the pathogen. Species of the pathogens reisolated from inoculated plants were confirmed to species by visual inspection of colonies (Blackwell, 1943; Erwin & Ribeiro, 1996; Gallegly & Hong, 2008; Kröber & Marwitz, 1993; Waterhouse & Waterston, 1966).

2.3 | Test 2. Stem inoculations

This test focused on testing both *P. tentaculata* and *P. cactorum* in an even comparison. Two isolates of each *Phytophthora* species were used.

2.3.1 | Plant conditions

Plants were flooded for 24 hr before inoculation, and then flooding conditions were maintained for 48 hr postinoculation. Following flooding, plants were watered at regular intervals.

2.3.2 | Pathogen inoculation treatment

The inoculation method used was similar to the one presented in Navarro, Sims, and Hansen (2015, Test 3). A 6-mm-diameter agar disc, containing mycelium and grown on V8 agar, was placed over a pinpricked stem approximately 10 cm above the soil line. Discs were excised from the growing edge of 7-day-old colonies of *P. tentaculata* and *P. cactorum*. Negative control inoculum consisted of 6-mm discs excised from sterile V8 agar. Two randomly selected isolates of *P. tentaculata* and of *P. cactorum* were used (Table 1), with one inoculation per plant. The inoculated area was wrapped using sterile Miracloth (Millipore), Parafilm®M sealing film and aluminium foil.

2.3.3 | Canker assessment

Lesion size (canker area in mm^2) was measured 14 days following inoculation. Aluminium foil, Miracloth (Millipore) and Parafilm®M were removed. The area of the stem was examined for canker symptoms by lightly scraping the outer bark to observe the inner bark and cambium for necrosis and dead tissue. The symptomatic area (length × width) was then measured to the nearest 0.5 mm in each direction.

2.3.4 | Reisolation

Following measurements, reisolation of the pathogen was performed from symptomatic tissue near the outer edges of each canker, and identification of each culture obtained was done to the species level as outlined in the methods of Test 1.

2.4 | Test 3. Stem inoculation and canopy evaluation of California sycamore

Test 3 focused on inoculations with *P. tentaculata* because of its invasive species status. This test focused on California sycamore because it was the important remnant species at the contaminated restoration of particular concern.

2.4.1 | Plant conditions

Plants were flooded for 48 hr prior to inoculation, and then flooding conditions were maintained for an additional 72 hr postinoculation. Following flooding, plants were not watered for the remainder of the test.

2.4.2 | Pathogen inoculation treatment

The inoculation method was the same as described for Test 2, but for this test, only California sycamore was inoculated. Three isolates of *P. tentaculata* and one of *P. cactorum* were used (Table 1).

2.4.3 | Canker assessment

Lesion size (canker area in mm^2) was measured 14 days following inoculation the same as described for Test 2.

2.4.4 | Canopy assessment

In addition to evaluating the size of cankers, the canopies of California sycamores were evaluated for symptoms including both chlorosis and wilting. Each leaf from the plant canopy of every plant was scored as symptomatic (with chlorosis and/or wilting) or healthy (no chlorosis and no wilting) 21 days postinoculations. The proportion of the canopy that was symptomatic was inferred by dividing the number of symptomatic leaves by the total leaves per canopy.

2.4.5 | Reisolation

Following measurements, the symptomatic tissue near the outer edges of each canker was plated, and the resulting colonies were morphologically identified to species level as described for Test 1.

2.5 | Statistical tests

2.5.1 | Statistical analysis for pathogenicity tests

All statistical analyses were performed in the R computing environment (R Core Team 2016), and effects were evaluated at the 95% confidence level. Different models systems were used to handle the distinct types of response variables in each test.

In Test 1, the nonparametric ordinal response was evaluated using the Kruskal–Wallis rank sum test (Hollander & Wolfe, 1973) to check for an effect of the overall pathogen treatment. Comparisons were also made among treatments for the mean disease rating and for the proportion of treatments with a ≥3 disease severity rating (Krause et al., 2001). In addition, summary statistics including the most frequent disease rating (mode) and the maximum disease rating are presented in Table 3.

To compare canker data from Test 2, each "plant species × pathogen isolate" was modelled using analysis of variance (Crawley, 2007). The natural logarithmic scale was applied to responses, then, following modelling, exponentiated back to the standard scale with the natural

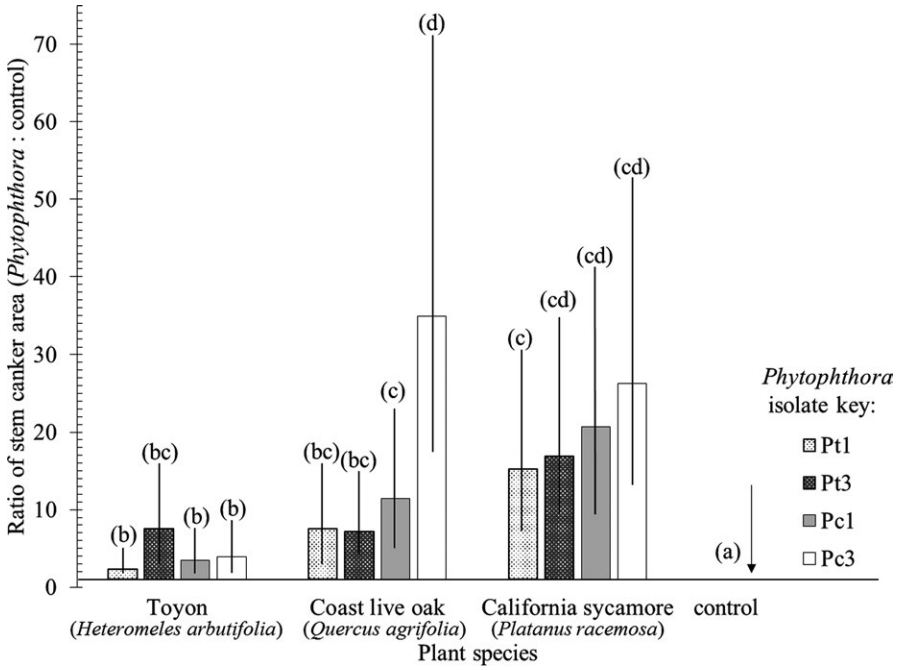

FIGURE 1 Cankers resulting from stem inoculations in Test 2 presented as the ratio of *Phytophthora* to control. Bar graphs are the estimated median, and error bars are the confidence intervals. Letters in parenthesis represent statistical groups

TABLE 4 California sycamore canopy symptoms resulting after each treatment in Test 3. Included is the estimated percentage of the canopy affected by *Phytophthora cactorum*, or *Phytophthora tentaculata*, the confidence intervals (CI) for these estimates and *p*-value for a difference from the control

Treatment	Estimate	Lower.CI	Upper.CI	*p*-Value*
Control	10%	3%	32%	–
P. cactorum	42%	24%	63%	0.029
P. tentaculata	36%	25%	49%	0.036

Note. *Difference from control inoculation.

antilog, that is, back-transformed, and the average ratio of the median canker between the inoculated and mock-inoculated control plants reported (Figure 1). In addition, the mean canker size and standard deviation for each isolate were calculated without the modelled log transformation and provided in the results text.

To evaluate canopy symptoms in sycamores inoculated in Test 3, the log odds of the proportion response was assessed with the logistical model function *glm*, *family = quasibinomial* (Dobson, 1990; Venables & Ripley, 2002) and was back-transformed to estimate the proportion and presented as a percentage (Table 4).

3 | RESULTS

3.1 | Test 1: Root inoculations

3.1.1 | Toyon roots

A summary of root symptoms including typical rating (mode) and maximum rating is included for the three plant species tested (Table 3). Phytophthora root disease was also evaluated based on the mean severity rating and proportion of plants with moderate root disease (proportion with severity rating ≥3, and mean severity >2 from Table 2). Phytophthora root disease on roots of inoculated toyons was significantly greater than that of controls ($p = 0.03$). Mean disease severity rating for *P. cactorum* was 2.8, and the moderately diseased proportion (≥3) was 0.8; mean severity rating for *P. tentaculata* was 2.2, and the proportion of plants with a disease rating ≥3 was 0.3. The mean disease severity rating of controls instead was 1.0, and the proportion of plants with disease rating ≥3 was 0.

3.1.2 | Coast live oak roots

Phytophthora root disease symptoms on inoculated coast live oaks were significantly greater than controls ($p = 0.001$). Mean disease severity rating for *P. cactorum* was 2.6, and the proportion of plants with a disease rating ≥3 was 0.6; mean severity rating for *P. tentaculata* was 3.0, and the proportion of plants with a disease rating ≥3 was 0.7. Mean severity rating of controls was 1.0, and the obviously diseased proportion was 0.

3.1.3 | California sycamore roots

Phytophthora root disease on inoculated California sycamore roots was significant ($p = 0.01$), but no cases of at least moderate disease (≥3) were recorded. Mean disease severity rating for *P. cactorum* was 1.2; mean severity rating for *P. tentaculata* was 1.7. The mean severity rating of controls was 1.0.

3.2 | Test 2: Stem inoculation results

3.2.1 | Toyon stems

Overall, size of cankers was significant ($p = 0.01$) when compared to controls, but their size was very small compared with the size of

cankers measured on the other two plant hosts (Figure 1). Average size of cankers (mm^2) and standard deviations caused by each isolate were as follows. Pt1: 5.6 ± 2.9; Pt3: 11.0 ± 5.9; Pc1: 8.0 ± 4.2; Pc3: 16.0 ± 18.4. Grouped by pathogen species and based on median values, the average ratio between canker area caused by the pathogen and canker area of the control was 4.68 for *P. tentaculata* and 5.01 for *P. cactorum*.

3.2.2 | Coast live oak stems

Significant cankers resulted from the stem inoculation test ($p < 0.0001$; Figure 1). Average size of cankers (mm^2) and standard deviations caused by each isolate were as follows. Pt1: 16.4 ± 9.0; Pt3: 16.4 ± 4.5; Pc1: 26.2 ± 14.5; Pc3: 84.4 ± 48.8. The average ratio of the median canker area from *P. tentaculata* was 7.48 and for *P. cactorum* was 23.67.

3.2.3 | California sycamore stems

Stem inoculations of California sycamore produced sizeable cankers, significantly different ($p < 0.001$) from the size of cankers in controls and in toyons (Figure 1). Average size of cankers (mm^2) and standard deviations caused by each isolate were as follows. Pt1: 53.2 ± 44.4; Pt3: 31.6 ± 4.3; Pc1: 43.8 ± 11.2; Pc3: 63.4 ± 27.5. The average ratio of the median canker resulting from inoculations compared to lesions caused by the mock-inoculations 13.26 for *P. tentaculata* and 19.33 for *P. cactorum*.

3.3 | Test 3: Stem inoculation and canopy evaluation results

3.3.1 | California sycamore stems

Cankers resulting from stem inoculations in Test 3 were significant when compared to controls ($p = 0.001$). Average size of cankers (mm^2) and standard deviations caused by each isolate were as follows. Pt1: 52.2 ± 19.1; Pt3: 29.1 ± 24.2; Pt4: 39.8 ± 31.1; Pc1: 70.3 ± 43.0.

3.3.2 | California sycamore canopy

The canopies of the California sycamore plants were evaluated for chlorosis and wilting, in addition to the evaluation of canker size. Using the average % of canopy symptoms of controls as baseline, the average percentages of symptomatic canopy were 32% and 26% more than in controls, for *P. cactorum* and *P. tentaculata*, respectively (Table 4).

3.4 | Reisolation from tests

Following an incubation period of up to 10 days at 18°C, plates were checked for reisolation success. The inoculated pathogen was reisolated from each plant in Tests 1 and 2. No reisolations were obtained from controls. The inoculated pathogen was reisolated from all but two test plants used in Test 3. Again, no reisolations were ever obtained from controls. In all cases, the same pathogen was reisolated which had been inoculated on the test plant, confirmed by comparison to isolates utilized.

4 | DISCUSSION

There is increasing evidence that emergent pathogens and pests may reduce the biodiversity of invaded ecosystems (Fisher et al., 2012). Perennial plants including trees and woody shrubs are particularly at risk because emergent pathogens are bound to exert a prolonged and repeated disease pressure on these hosts due to their extended lifespan (Brasier & Scott, 1994; Fisher et al., 2012; Maloy, 2005; Shearer & Tippett, 1989). The recently reported presence of a putatively exotic *Phytophthora* species comingled with a pathogen species possibly native to portions of California provided a unique opportunity to compare whether broad differences in biogeographical history of two pathogen species may result in differences in the degree and type of disease they cause. We selected three hosts important in the California ecosystems where *P. tentaculata* and *P. cactorum* have recently been introduced (Rooney-Latham et al., 2015) to compare the virulence and type of disease caused by the "new" (*P. tentaculata*) and the "old" pathogen species (*P. cactorum*). It should be noted that, although putatively native to parts of California, *P. cactorum* is not known from the dry grasslands and riparian forests of the San Francisco East Bay. However, as no baiting or water filtration was performed prior to outplanting nursery stock, it is possible that *P. cactorum* could be present at low quantities either due to an introduction event long ago or because it is a native species.

Although the length of our trials was relatively short (i.e., 14–30 days), the choice of such length was dictated by the relatively small size of the plants tested. In all trials, the severity of symptoms was significantly different between treatments and controls, further indicating that the length of the experiments was sufficient to draw conclusions, and saved us the unnecessary use of resources associated with longer trials. Additionally, it should be pointed out that other researchers have routinely performed experiments of comparable length to assess the virulence of *Phytophthora* species (Eyre, Hayden, Kozanitas, Grünwald, & Garbelotto, 2014) including *P. cactorum* (Lilja, Karjalainen, Parikka, Kammiovirta, & Nuorteva, 1998) and *P. tentaculata* (Meng & Wang, 2008; Rooney-Latham & Blomquist, 2014). Although mortality (a qualitative variable) can be assessed using longer experiments, quantitative variables including canker size and severity of canopy symptoms are often biased in longer trials, because the size of lesions and the appearance of the canopy cannot be considered reliable when plants are dead. Finally, our inferences are all based exclusively on *comparative* results obtained in the same time period, inoculating at the same time genotypes of two distinct *Phytophthora* species onto up to three host species.

Our first hypothesis stated that, based on previous reports limited to *P. cactorum* only (Keim et al., 1976), toyon would be susceptible to root and collar disease caused by *P. tentaculata* and *P. cactorum*. Results confirmed that the root systems of toyons were highly

susceptible to both *Phytophthora* species, although infected plants displayed a remarkably large range of disease severity. Variability of disease severity in controlled tests has been observed in previous studies as well, and it has been postulated to result in patches of dead and surviving plants in infested areas (Keim et al., 1976).

Our second hypothesis stated that coast live oak would be susceptible to both *P. tentaculata* and *P. cactorum*, and disease would develop both in the roots and in the stems. Indeed, significantly large cankers were caused by each pathogen both on stems and roots (Figure 1). The evidence gathered proved that both *P. tentaculata* and *P. cactorum* can cause sizeable stem cankers and significant root infection in coast live oak. Trunk cankers from *P. cactorum* on coast live oaks have already been reported (Mircetich, Campbell, & Matheron, 1977). However, our results further showed that: (a) *P. tentaculata* was not more aggressive than *P. cactorum* in aerial portions, and, (b) a substantial difference in pathogenicity was detected between the two *P. cactorum* isolates. High variability when comparing genetically different isolates of *P. cactorum* is not unusual (Bhat, Colowit, Tai, Aradhya, & Browne, 2006; Hantula, Lilja, Nuorteva, Parikka, & Werres, 2000; Hantula, Lilja, & Parikka, 1997). However, recently significant phenotypic variability between genetically identical populations of the pathogen has been demonstrated for *Phytophthora ramorum* (Garbelotto et al., 2015; Kasuga et al., 2012) and warrants a possible route of future investigation for these particular *Phytophthora* species.

Our third hypothesis stated that California sycamore might be susceptible to both *P. tentaculata* and *P. cactorum*, but the roots may be rather resistant. Consistent with our hypothesis, *P. cactorum* and one of two of the *P. tentaculata* isolates produced few or no symptoms in the inoculated roots system (Table 3). However, both pathogens could be reisolated from them, suggesting that roots are not immune to infection, even if showing limited symptoms. Differently from roots, both *Phytophthora* species caused significant cankers on stems of sycamores both in Tests 2 and 3. This result is noteworthy because it suggests that even with minimal stem injury (stem was only pinpricked and not inoculated under wounded tissue) disease of sycamore trunks could develop in the presence of *Phytophthora* propagules splashed on stems. Splashed inoculum is extremely common for both aerial and soilborne *Phytophthoras*. For species in the first category, splash inoculum can be contained in water droplets that are produced on aerial portions of the infected plants and can be released during wind and rain events (Davidson, Wickland, Patterson, Falk, & Rizzo, 2005; Ristaino & Gumpertz, 2000). Splash inoculum of soilborne *Phytophthora* species is also a major pathway of spread and can lead to rapid rates of disease increase (Ristaino & Gumpertz, 2000): In this case, inoculum can be spread onto aerial parts of plants either mechanically through tools or overhead irrigation, by human or animal vectors, or simply by water droplets that splash as rain (or irrigation water) bounces on soil, plant and water surfaces. Notable examples of soilborne *Phytophthora* species spreading through a splash mechanism include *P. cactorum*, *P. palmivora*, *P. megakarya*, *P. syringae*, *P. botryosa* and *P. lateralis*, just to cite a few (Erwin & Ribeiro, 1996; Gregory, Griffin, & Maddison, 1984; Madden, Wilson, Yang, & Ellis, 1992; Robin et al., 2011; Trionne & Roth 1957). We conclude that in stands of *P. racemosa* infested by *Phytophthora* spp., it may be critical to avoid or minimize splash: This means that any work and vehicular or human transit should be strongly discouraged during wet spells.

Our final hypothesis overarched across all trials performed in this study and stated that on each of the three tested hosts, *P. tentaculata*—being an exotic species of recent introduction—may be more virulent than *P. cactorum*. Overall, results of our trials did not substantiate this hypothesis. In general, in fact, both *P. tentaculata* and *P. cactorum* were similarly moderately aggressive, suggesting that both species represent a potential threat to these three native plant species, but may require drying stress in some cases conditions common in California. However, only 2–4 genotypes of each pathogen species were used, and, presumably, plants purchased came from a single or a few populations. Further studies of the genetic diversity of both the host and the pathogen are warranted to determine whether: (a) Truly, as we had originally postulated, coevolution to the genus could convey some level of resistance to new congeneric invaders; (b) *P. cactorum* may include genetically different populations, some of which may indeed be exotic to plant populations from *P. cactorum*-free areas, thus having the same virulence as an exotic pathogen such as *P. tentaculata*; (c) founder effects bound to decrease genetic diversity may be involved in the limited virulence observed for *P. tentaculata*.

Nonetheless, significant intraspecific variability in virulence was identified, despite the low number of pathogen genotypes employed. Intraspecific differences, particularly if detected when using a small number of genotypes, indicate that multiple introductions of different isolates can result in very different outcomes. Hence, the repeated release of any given *Phytophthora* species should be avoided. Isolates belonging to the same species may differ greatly in their virulence because of genetic isolation among populations leading to drift and differentiation (Grünwald et al., 2008), because of adaptive introgression of virulence-related genes through hybridization with related species (Brasier & Buck, 2001; Brasier et al., 2004; Schardl & Craven, 2003), or because the different history of identical genotypes may lead to phenotypic diversification (Kasuga et al., 2012).

Restoring wildlands is performed with the intent of bringing them to a state that reflects nearby remnant healthy sites, but achieving this goal will be much more costly, and in some cases impossible, with the introduction and possible subsequent invasions of emergent plant pathogens such as *P. tentaculata* and *P. cactorum*. Our results suggest that *Phytophthora* species already introduced or native in wildlands in the west coast of the United States should be reconsidered as biological threats, so as to stop reintroducing them back into ecosystems, and into new ones as wildlands in California are not homogeneous. The tests herein do not suggest *P. cactorum* or *P. tentaculata* would likely be as virulent as *P. ramorum* or *Phytophthora cinnamomi* (Frankel & Palmieri, 2014; Garbelotto, Hüberli, & Shaw, 2006; Garbelotto, Svihra, & Rizzo, 2001). Instead these and a long list of other *Phytophthora* species are pervasive

(Bourret et al., 2018; Sims et al., 2015) and can cause disease symptoms and display intraspecies virulences dynamics and in this way can be quite insidious.

Because both pathogens were likely introduced through infected nursery stock (Rooney-Latham et al., 2015), intense and critical screening should be implemented, as well as changes to nursery production standards for containerized plants (Griesbach, Parke, Chastagner, Grünwald, & Aguire, 2012; Schweigkofler, Kosta, Huffman, & Suslow, 2014; Sims, Conforti, Gordon, Larssen, & Steinharter, 2016). Where possible, seeds should be used as a preferred alternative to containerized plants during restoration efforts. These additional efforts may also minimize the creation of new pathogens through interspecific hybridization, a phenomenon whose frequency is rising in nursery environments (Yang, Richardson, & Hong, 2014). Riparian species like California sycamore may have root systems that have been selected for *Phytophthora* tolerance, but with the addition of greater disturbances leading to stem damage and exposure to inoculum of introduced *Phytophthora*, aerial diseases may be expected. These disturbances should be minimized if possible. In addition, riparian species may require drying stress for apparent above ground symptoms. Finally, evergreen, drought-adapted plants like toyons or coast live oaks (Morrow & Mooney, 1974; Steinberg, 2002) may display minimal above ground symptoms, even when Phytophthora root disease severity is moderate to severe which could lead to rapid unexpected death following transplant into drier locations, or lingering in wetter ones.

In conclusion, knowledge of the ecology and history of a host can help to predict the type of disease caused by *Phytophthora* species on such a host. History inferred through published literature helped to predict that toyon would have susceptible roots but few aerial symptoms, a combination that could make this host a candidate as an introduction pathway for *P. cactorum* or *P. tentaculata* into wildlands, if the infected plant–pathogen system survives. In dry locations spread could be relatively limited without flooding, drainage that contacts infected plant roots and carries inoculum to other plants, or direct root-to-root contact. In wet locations spread or survival could be more pervasive, but symptoms may be less obvious. Understanding the ecology of a riparian species like California sycamore helped us predict disease tolerance in its root systems, but susceptibility in its aerial portions. This knowledge informed us that introducing a novel *Phytophthora* species and increasing splash of its inoculum may lead to disease of aerial portions of this host. This prediction has recently become true, when dead and symptomatic planted California sycamores in a restoration site were found to harbour a stem infection by a soilborne *Phytophthora* species (Sims and Garbelotto, unpublished data). If infected plants were used in riparian restoration, it could lead to inoculum in streams, especially if infected roots are maintained and in contact with stream water. During floods inoculum could (a) be unsuccessful, (b) move to other susceptible streambank plants, or (c) following contact with plant stems cause aerial infections. The tubes used to protect and surround restoration plants, in flooding conditions, could hold flooded water and inoculum on stems longer and make spread to other plants less likely. However, it would also likely increase the chance of success of the aerial infection on that plant. We have also learned that, due to intraspecific variation in virulence levels independent of the exotic or endemic origin of a pathogen, multiple introductions of different genotypes of the same species or of different species should be avoided. The value of these predictions is that they can be formulated even when only preliminary pathogenicity data are available, thus allowing for the timely implementation of appropriate disease mitigation strategies.

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