Distribution of *Phytophthora ramorum, P. nemorosa,* and *P. pseudosyringae* in Native Coastal California Forest Communities[1]

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Abstract

Phytophthora ramorum, causal agent of sudden oak death, is well established over approximately 450 km of native forest along the California coast. In the course of research on this invasive exotic pathogen, two other putatively exotic aerial *Phytophthora* species, *P. nemorosa* and *P. pseudosyringae*, were discovered (Ivors and others 2004, Linzer and others 2006). Little is known about the ecology and biology of these other species and how they interact with *P. ramorum*. Preliminary research has found that *P. nemorosa* and *P. pseudosyringae* have similar host and geographic ranges and cause similar disease symptoms as *P. ramorum* (Hansen and others 2003, Murphy and Rizzo 2006, Wickland and Rizzo 2006). However, *P. nemorosa* and *P. pseudosyringae* do not appear to cause landscape level mortality of oaks (*Quercus* spp.) or tanoak (*Lithocarpus densiflorus*) and infect fewer plant species, as does *P. ramorum.* Additionally, while all three pathogens are patchy over the landscape, *P. nemorosa* and *P. pseudosyringae* are distributed over a broader geographical area than *P. ramorum,* extending into the Sierra Nevada. Symptoms caused by these three species are indistinguishable in the field and the causal species can only be identified using either molecular methods or microscopically once cultured.

A plot study was established to determine the distribution and incidence of *P. ramorum*, *P. nemorosa* and *P. pseudosyringae* in coastal forest communities, and to relate pathogen presence to community, structural, and environmental variables. A total of 499 circular, 1/20 ha (500 m^2) plots were established at 38 sites throughout central and northern coastal California with 2 to 38 plots per site (Fig. 1). Field plots were installed during the spring and summer months between 2001 and 2005. The majority of sites are in national, state, county, and regional parks with several sites on university reserves and private properties. Plots were established within four native forest alliances: coast redwood, coast live oak, mixed oak, and Douglas-fir-tanoak forests (Sawyer and Keeler-Wolf 1995). Each of these forest communities contains numerous hosts of *P. ramorum* and at least two hosts of *P. nemorosa* and *P. pseudosyringae*. California bay laurel (*Umbellularia californica*) is the only species that overlaps all four plant communities. All three pathogens have the potential to spread and effectively infest all four forest communities and essentially interact within the same ecological niche. It is important to note that California coastal forests are very heterogeneous with many ecotones, so transitions between forest types can occur rapidly, contributing to the patchy distribution of these pathogens. Plots were placed in a stratified random design and indiscriminately regarding presence or absence of *Phytophthora* species. The locations were selected to represent a broad geographical range, a variety of aspects and forest community types, and areas with minimal human disturbance. Each plot was evaluated for plant species

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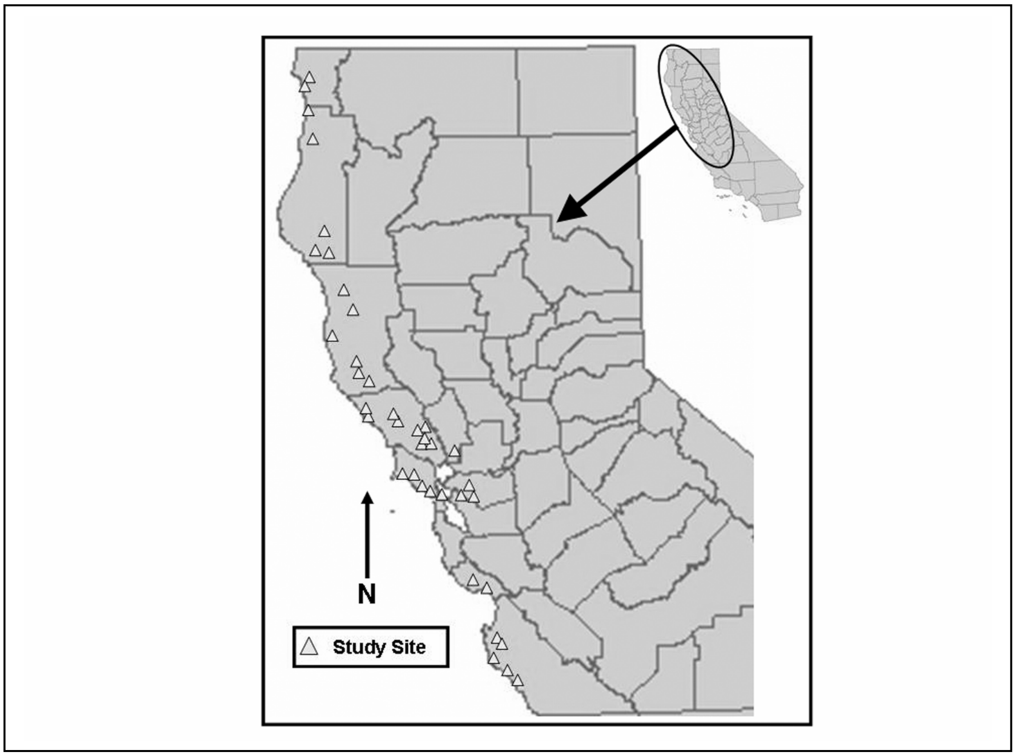

Figure 1—Map of all study sites in California where each triangle represents a single sample site. Polygons within the state represent county line designations.

composition, forest structure and environmental variables, and incidence of aerial *Phytophthora* species. Over 21,000 trees and shrubs were measured and examined for presence of aerial *Phytophthora* species. Any symptomatic aerial plant tissue (leaf or twig/trunk cankers, up to 10 to 15 leaves or canker pieces per individual) was collected and plated onto *Phytophthora*-selective medium (PARP). Plates were incubated at 20°C and checked microscopically twice weekly for one month to visually confirm presence of *Phytophthora* species.

Phytophthora ramorum was recovered from 40 percent of plots at 22 sites, with *P. nemorosa* and *P. pseudosyringae* recovered from 18 (16 sites) and 13 (11 sites) percent of plots, respectively. *P. ramorum* and *P. nemorosa* were found together on 55 plots, and were both isolated from the same tree 137 times, primarily on bay laurel (75.2 percent) but also on coast redwood (*Sequoia sempervirens*) (14.6 percent), tanoak (9.5 percent), and Douglas-fir (*Pseudotsuga menziesii*) (0.7 percent). *Phytophthora ramorum* coexisted with *P. pseudosyringae* on nine plots at five sites. These two species were isolated from the same bay laurel tree on six different plots. All three *Phytophthora* species were recovered on the same plots and from the same bay laurel tree twice at different sites. Sixteen sites were free of *P. ramorum* and include nine sites that are within 25 km of *P. ramorum* infestation. No *Phytophthora* species were detected on 220 plots and eight sites were pathogen free. Five of the sites that were *Phytophthora* free also had no bay laurel present. *P. ramorum*, *P. nemorosa,* and *P. pseudosyringae* were found in all four forest alliances. No other aerial *Phytophthora* species were identified during the course of this study.

A classification and regression trees (CART) analysis was used to identify potential pathogen predictor variables. CART analysis, a type of non-parametric statistical method, has advantages in ecological studies due to its ability to handle non-linear data well and not be constrained by distribution assumptions (Breiman and others 1984, De'Ath and Fabricius 2000). CART is a method used to explore differences among groups. The goal with CART is to partition data into homogeneous groups, creating a tree-like classification key to predict probabilities of a response variable by selecting the most explanatory predictor variables. This objective is achieved by "growing" an overly large tree, which is then "pruned" to a parsimonious size using a cross validated cost complexity approach. CART results are visually intuitive, making them ideally suited to analyze complex ecological data.

In this study, many environmental, forest structure, and plant community variables were used to create models to predict a probabilities of each *Phytophthora* species presence or absence. The selected CART models predict the greatest probabilities of *P. ramorum* occurring at sites closer to a source of *P. ramorum* inoculum, those with greater average winter or spring precipitation, sites with any bay laurel present, and those with more moderate climates (lower maximum annual temperatures, lower solar radiation, and higher minimum annual temperatures). Similarly to *P. ramorum*, reduced annual maximum temperature, increased bay laurel abundance, and greater winter precipitation all predicted greater probability of *P. nemorosa* presence. However, reduced annual minimum temperature additionally predicted greater *P. nemorosa* presence. This concurs with lab studies that have demonstrated this pathogen's lower temperature optimum than the other *Phytophthora* species (Hansen and others 2003). In contrast to *P. ramorum* and *P. nemorosa*, the major branch for the selected CART tree predicting *P. pseudosyringae* presence was reduced average winter precipitation. *Phytophthora pseudosyringae* has been shown to be associated with drier plant communities (for example coast live oak forest type) and sites further inland from the coast (Wickland and others, unpublished).

As with previous studies, increased abundance and density of bay laurel (calculated as importance value [IV]), a reservoir host that supports high sporulation, was found to increase the probability of *P. ramorum* occurrence; a similar relationship with bay laurel was noted for *P. nemorosa* and *P. pseudosyringae* (Maloney and others 2005, Murphy and Rizzo 2006, Wickland and Rizzo 2006). Pathogen presence was highly related to forest structure, climate, and biophysical variables, although the patterns varied by species. While the probabilities of all three pathogens increase with more bay laurel present, they differ in their responses to various climatic variables, including precipitation and temperature (table 1).

Table 1—Summary of selected CART model predictor variables and the condition that increases the probability of presence of the corresponding aerial *Phytophthora* species. The selected predictor variables occur most often between the selected models for all three *Phytophthora* species. Pr= *P. ramorum;* Pn= *P. nemorosa;* Pps= *P. pseudosyringae*

Selected CART Variable	Variable Condition	Pathogen
Bay Presence (IV)	High	Pr, Pn, Pps
Winter/Spring Precipitation	High	Pr,Pn
Winter Precipitation	Low	Pps
Maximum Annual Temperature	Low	Pr,Pn
Minimum Annual Temperature	High	Pr
Minimum Annual Temperature	Low	Pn
Summer Solar Radiation	Low	Pr

While the three *Phytophthora* species occupy similar host and geographical ranges as well as the same forest communities, they differ in their specific ecological niches and impacts on coastal forests. Results from this study provide additional information about the distribution of *P. ramorum*, including location and intensity of sudden oak death within state and regional parks, as well as initial distribution information about *P. nemorosa* and *P. pseudosyringae*. This is the first study to examine the ecological associations between these three *Phytophthora* species, across a wide geographic distribution and within several forest communities. These plots are a portion of a permanent plot network that will continuously monitor pathogen infestation, and address future research questions regarding forest dynamics and ecological impacts as a result of these pathogens.

Key words: *Phytophthora ramorum*, forest *Phytophthora* species, sudden oak death, forest ecology, invasive species, California forest communities, classification and regression trees, CART analysis.

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