Sudden Oak Death in California: What Is the Potential?

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Sudden oak death, a disease associated with the pathogen *Phytophthora ramorum*, has a large number of shrub and tree host species. Three of the tree species most susceptible to mortality from the disease, California black oak (*Quercus kelloggii*), coast live oak (*Quercus agrifolia*), and tanoak (*Lithocarpus densiflorus*), are estimated to predominate by basal area on 1.52 (\pm 0.10) million ac in 12 counties that currently are under quarantine for the disease. The variety, prevalence, and importance of host species to wildlife indicate a high potential for impact on forest ecosystems in California.

Keywords: forest monitoring, forest health, ramorum dieback, ramorum leafblight

n April 1995, homeowners contacted the University of California Cooperative Extension office in Marin County to inquire as to why more than a dozen nearby tanoaks were dying (Svihra 2001). It was not until 7 years and tens of thousands of dead trees later that a plant pathologist was able to isolate the associated pathogen, Phytophthora ramorum (Rizzo et al. 2002). By January 2005, the disease had spread to forests in 14 California counties and one county in Oregon, and the USDA reported that samples from nurseries in 22 states (Alabama, Arkansas, Arizona, California, Colorado, Connecticut, Florida, Georgia, Louisiana, Maryland, New Jersey, New Mexico, New York, North Carolina, Oklahoma, Oregon, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, and Washington) had all tested positive for the pathogen (Animal and Plant Health Inspection Service [APHIS] 2005). A number of states and Canada implemented restrictions on entry of plants from California (APHIS 2005).

ABSTRACT

Much remains unknown about *P.* ramorum, including the genetic resistance of host species, the effects on mortality and growth, the environmental conditions necessary for establishment, and the ultimate

potential range of the disease. The disease has been commonly labeled "sudden oak death" (SOD) although the dozens of known hosts include many nonoak trees and shrubs. Tree hosts include bigleaf maple (Acer macrophyllum), California buckeye (Aesculus californica), Pacific madrone (Arbutus menziesii), tanoak (Lithocarpus densiflorus), Douglas-fir (Pseudotsuga menziesii), coast live oak (Quercus agrifolia), canyon live oak (Quercus chrysolepis), California black oak (Quercus kelloggii), coast redwood (Sequoia sempervirens), and California bay laurel (Umbellularia californica). Other nontree hosts include many very common species and genera such as manzanita, rhododendron, wood rose, California honeysuckle, and evergreen huckleberry.

Some host species, such as Douglas-fir and coast redwood, seem to show little effect from the disease, at least in mature trees (Garbelotto et al. 2003). Other hosts, such as tanoak, California black oak, and coast live oak, are more likely to die after infection (Garbelotto et al. 2003), although mortality can be patchy (Kelly and Meentemeyer 2002, McPherson et al. 2002).

It may be many years before the full effects of the disease are known. However, estimating the extent of forestland containing known host species can provide some indication of the potential magnitude of the disease. In this article, we assess California forests that contain tree species that are host species for *P. ramorum*. Estimates of stand density, structure, and environmental characteristics of forest stands with host species present are provided and compared with locations where symptoms have been observed. These preinfestation forest attributes will establish a baseline for future monitoring of the pathogen and its impacts.

Methods

Twelve California counties-Alameda, Contra Costa, Humboldt, Marin, Mendocino, Monterey, Napa, San Mateo, Santa Clara, Santa Cruz, Solano, and Sonomawere quarantined because of the presence of P. ramorum as of June 2004 and constituted the analytical region (Figure 1).¹ Three Forest Service inventories were combined to make preinfestation estimates: one 1996-1998 inventory of national forests in the selected counties and two 1991-1994 statewide inventories, one of woodland and one of timberland on private (and some public) lands. The first inventory was conducted by the National Forest System, Pacific Southwest Region, and the latter two inventories were conducted by the Forest Inventory and Analysis program of the Pacific Northwest

¹Disease incidence and the quarantined area have continued to expand since we conducted our analysis; interested readers may wish to obtain current information for these from APHIS (2005) and the California Oak Mortality Task Force (2005).

and Pacific Southwest Research Stations. Forestland in national and state parks and some other reserved areas was not included in this assessment because forest inventory data were not available for those lands. Although exact figures were not available, information from managers of these lands indicated that uninventoried forest was about 8% of total forestland within the 12 counties.

All three inventories included a remote sensing phase and a field sampling phase. Depending on the inventory, we used either stratified estimation or double sampling for stratification to produce estimates (Barrett 2004). Each inventory used a sample unit composed of five subplots, with variable radius sampling for most trees on the subplot and fixed radius sampling on a smaller area to measure small diameter trees. Estimates for forestland were made by two different methods, either (1) classifying the forest type of the plot to the tree species that was predominant by basal area or (2) calculating characteristics of forestland where a particular tree species was present. The former method is useful for understanding attributes where a particular species is predominant, and the latter method is useful for understanding attributes throughout the geographic range where the species occur. Species' presence indicates that at least one tree of that species, of any size, was inventoried on forested conditions within the plot. All attributes were derived from field measurements, with the exception of precipitation, which was estimated by overlaying plot locations with a geographic information system theme of 1961-1990 average annual precipitation (Spatial Climate Analysis Service 2004).

Most estimates reported here are produced from the full set of 743 forested inventory plots in these counties and represent predisease conditions from the 1990s. In addition, in 2001 and 2002 field crews recorded symptoms and collected samples on 155 plots that had been prescreened for the presence of Quercus or Lithocarpus host species. Definitive sampling for P. ramorum proved difficult, because the 2001-2002 lab procedures are now thought to have produced high levels of false negatives from ooze samples and reliable results from leaf samples were possible only for California bay laurel. Thus, results are based on field crew classification of plots as "SOD suspected" based on observations of stem and



Figure 1. Plot locations with California black oak, tanoak, or coast live oak trees. Quarantined counties (summer 2004) are shown in yellow.

branch cankers or foliar lesions on host tree species.

Results and Discussion

Of the 155 field plots visited, 31 were classified as SOD suspected and 124 plots did not show symptoms. The corresponding population estimate for the quarantined area is that there were 220,000 (\pm 40,000) ac of forestland where host species showed symptoms in 2001–2002. Although this is the best estimate that can be made with available data, any confusion of SOD symptoms with similar diseases would contribute to overestimating affected land, and the lack of samples from reserved areas would contribute to underestimation. A comparison of the 31 SOD-suspected plots to the remaining 124

plots showed no significant difference of initial (1991–1995) conditions of trees per ac (P = 0.0945), average crown ratio (P = 0.2557), pre-1990s mortality (P = 0.8035), or basal area (P = 0.0556).

Among other factors, the ultimate effect of the disease on forestlands will be limited by the range of host species. Within the 12-county area in the 1990s, there were an estimated 3.86 million forested ac $(\pm 3\%$ sampling error [SE]) where a listed *P. ramorum* host species was the predominant tree species by basal area (Figure 2). Eighty-three percent of this area was privately owned. Most of this forest was dominated by host species such as Douglas-fir and redwood, which do not appear to be susceptible to trunk lesions and associated mortality, at



Figure 2. Forest area by predominant species for counties of Alameda, Contra Costa, Humboldt, Marin, Mendocino, Monterey, Napa, San Mateo, Santa Clara, Santa Cruz, Solano, and Sonoma.

Table 1. Preepidemic attributes for *P. ramorum* host tree species in California, within the listed 12-county area (Alameda, Contra Costa, Humboldt, Marin, Mendocino, Monterey, Napa, San Mateo, Santa Clara, Santa Cruz, Solano, and Sonoma counties), excluding state and national parks.^a

Species	Total trees (millions)	Average volume ⁶ (MBF/ac)	Average basal area ^{6,c} (ft ² /ac)	Average snag density ^{6,d} (trees/ac)	Average annual precipitation [#] (in.)	Total area present (1,000 ac)
Tanoak	210 ± 16	9±1	134 ± 18	68 ± 19	61 ± 7	2,473 ± 83
Redwood	115 ± 9	33 ± 5	230 ± 30	50 ± 9	50 ± 6	1,501 ± 77
Douglas-fir	112 ± 7	23 ± 3	159 ± 19	53 ± 9	62 ± 7	3,158 ± 91
Coast live oak	47 ± 7	3 ± 1	93 ± 20	21 ± 9	33 ± 7	899 ± 87
Canyon live oak	40 ± 7	5±2	121 ± 38	17 ± 7	55 ± 17	1,087 ± 87
Pacific madrone	62 ± 7	6 ± 2	104 ± 34	44 ± 16	49 ± 15	$2,255 \pm 111$
California laurel	39 ± 7	5 ± 2	108 ± 40	22 ± 14	48 ± 17	$1,318 \pm 102$
California black oak	32 ± 5	4 ± 1	88 ± 29	7±4	50 ± 16	995 ± 86
Bigleaf maple	12 ± 3	5 ± 4	84 ± 48	38 ± 32	45 ± 26	521 ± 66
Buckeye	6 ± 2	2 ± 3	87 ± 88	na	37 ± 38	328 ± 60
All host species	675 ± 28	16 ± 1	149 ± 8	46 ± 5	53 ± 3	$4,485 \pm 120$
Nonhost species	141 ± 11	4 ± 1	68 ± 8	24 ± 7	42 ± 5	$2,939 \pm 131$
All tree species	816 ± 29	13 ± 1	129 ± 6	41 ± 4	50 ± 2	4,989 ± 126

" Values following " ±" are sampling error for the estimate.

⁶ Volume per ac, basal area per ac, anags per ac, and average annual precipitation were calculated for forests where the species was

predominant by basal area. Calculated from trees greater than 5 in. dbh.

^d Snags are dead trees greater than 9 in. dbh and 7 ft in height.

least when trees are mature. Less than onequarter of forestland in these counties was dominated by nonhost species such as blue oak and Oregon white oak.

Tanoak, coast live oak, and California black oak, which are subject to lethal trunk infections (Garbelotto et al. 2003), predominated by basal area on 1.5 million ac (\pm 7% SE; Figure 2) in the 12-county area. There were an estimated 675 million *P. ramorum* host species trees with dbh greater than 5 in., including 210 million tanoak trees, 47 million coast live oak trees, and 32 million black oak trees (Table 1). Tanoak, coast live oak, and California black oak are not important commercial timber species, but they are very important for wildlife. The California Department of Fish and Game (2002) lists 28 mammals and 22 birds that feed on acorns. Tanoak and California black oak are the primary source of acorns in timberlands in the affected region. Tanoak trees, which predominated by basal area on 890,000 ac, were estimated to be a component of an additional 1,580,000 ac of mostly Douglas-fir and redwood forest. California black oak trees, which predominated by basal area on 160,000 ac, were estimated to occur on an additional 830,000 ac of other forest types.

Average volume, average basal area,

snag density, and average annual precipitation varied widely among areas where different P. ramorum host species predominated (Table 1) or were present. In contrast, for a given host tree species, many forest attributes were extremely similar between the quarantined counties and the rest of California. For example, the quarantined area where Douglas-fir was found was similar to the nonquarantined area where Douglas-fir was found in average density (162 ft² per acre of basal area versus 164 ft² per acre of basal area), in average number of trees (188 trees per ac versus 183 trees per ac), in average volume (20.1 thousand board feet (MBF) per acre versus 23.0 MBF/ac), and in average precipitation (55 in./year versus 52 in./year). Other host species also showed similarity in attributes between the quarantined and nonquarantined area.

The 10 tree hosts examined here are found on more than 4.4 million ac within the quarantined area and also are found on an additional 11.8 million forest ac in the rest of California (Table 2). Host species' presence is only one factor contributing to disease potential, and other factors such as climate may reduce or eliminate risk. Meentemeyer et al. (2004) developed a climate suitability index for the disease that gave high values to large sections of coastal counries in California and lower values for northern interior and Sierra Nevada forests in the state. When more is known about the biology and methods of transmission for the disease, it will be important to examine whether additional forest characteristics such as length of summer dry period or absence of understory host plants may limit the potential of spread to forests outside of the quarantined region.

Conclusion

We estimated *P. ramorum* host tree species were predominant by basal area on 10.1 million ac of California forestland. Predisease stand structure characteristics such as basal area and trees per ac were similar for susceptible forest types between areas where symptoms were observed and not observed. Characteristics also were similar for susceptible forest types between quarantined counties and the rest of the state. Improved lab tests for the presence of *P. ramorum* and ongoing monitoring of permanent plots throughout the state should increase our knowledge about the future course of the disease.

The California tree species most af-

Table 2. Estimates for *P. ramarum* host tree species in 48 California counties outside the known-infested guarantine zone.^{*a,b*}

Species	Area present (1,000 ac)	Area predominant by basal area (1,000 ac)	Trees with dbh over 5 in. (millions)
Tanoak	1,093 ± 76	194 ± 24	61 ± 8
Redwood	153 ± 33	54 ± 21	6 ± 2
Douglas-fir	$7,094 \pm 131$	$3,111 \pm 76$	339 ± 12
Coast live oak	609 ± 68	495 ± 56	37 ± 8
Canyon live oak	4,950 ± 155	$1,389 \pm 80$	269 ± 16
Pacific madrone	1.627 ± 89	45 ± 10	35 ± 4
California laurel	614 ± 76	33 ± 3	7 ± 2
California black oak	6.232 ± 161	818 ± 50	185 ± 10
Bigleaf maple	1.108 ± 79	62 ± 16	25 ± 5
Buckeye	804 ± 101	89 ± 30	16 ± 4
All host species	11.843 ± 200	6.290 ± 134	960 ± 28
Nonhost species	21.317 ± 195	15.002 ± 164	1.838 ± 33
All tree species	22,337 ± 189	$21,292 \pm 146$	$2,819 \pm 41$

* Excludes reserved lands outside of national forests, such as state and national parks.

⁶ Values following "±" are sampling error for the estimate.

fected by SOD-tanoak, California black oak, and coast live oak-are not particularly valued for timber production. In fact, tanoak is an aggressive competitor to Douglas-fir and redwood, and many landowners have attempted to rid their lands of it. Thus, some may view the disease as a problem that is severe for nurseries but not necessarily alarming for California forests. However, hundreds of thousands of dead trees in the landscape increase the risk of fire and insect attacks. Transportation of forest and nursery products has already been restricted. The long-term effect of leaf and branch infections on other host tree species is unknown. Commercially valuable species in other parts of the country-notably, in the South and East-also may be susceptible.

Of great concern is the potential effect on wildlife. Acorns from tanoak, California black oak, and coast live oak trees provide food for dozens of wildlife species, including bears, woodpeckers, deer, turkeys, mice, and flickers. Oak trees also provide nesting and denning sites. These three host species are extremely common (Figure 2) and are estimated to be found on 3.8 million ac of forestland within the 12-county area where *P.* ramorum is present, with 289 million trees larger than 5 in. dbh. A substantial reduction in numbers of these three species would affect hundreds of thousands of acres of wildlife habitat. The widespread distribution of *P. ramorum* host species indicates that very substantial direct and indirect effects on California forest ecosystems could occur from this disease.

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