

Impacts of *Phytophthora ramorum* on Oaks and Tanoaks in Marin County, California Forests Since 2000¹

Brice A. McPherson,² David L. Wood,² Maggi Kelly,² Sylvia R. Mori,³ Pavel Svihra,⁴ Andrew J. Storer,⁵ and Richard B. Standiford⁶

Abstract

The forests of Marin County were among the first in coastal California to be affected by the *Phytophthora ramorum* epidemic. Although initially observed in 1994 in tanoaks (*Lithocarpus densiflorus*) and 1995 in coast live oaks (*Quercus agrifolia*), it is evident from studies of disease progression that the pathogen was present at least several years prior to the first recorded tree mortality (Rizzo and Garbelotto 2003; McPherson and others 2005). The causal agent had not been identified in March 2000 when we established 20 plots in two Marin County sites, China Camp State Park, (CCSP, coast live oaks and California black oaks, *Q. kelloggii*) and the Marin Municipal Water District watershed (MMWD, all three species). Plots were between 320 m² and 3600 m², with a mean of 1234 (SE = 199) m². The goal of the study was to monitor disease progression (McPherson and others 2000) and, in particular, to understand the phenomenon of the abundant beetle attacks observed on bleeding trees. Plots were evaluated four times per year until March 2003, then twice annually thereafter. Through March 2008, every stem > 5 cm diameter at breast height (DBH) was evaluated for signs and symptoms of sudden oak death (SOD): bleeding, beetle attacks, and the presence of the fungus *Hypoxylon thouarsianum*. In 2001 and 2007, we recorded the basal area for every woody species with stem DBH > 5 cm found within 0.08-ha subplots placed within the larger plots.

Mortality of each of the three species has increased steadily since 2000. Calculated infection and mortality rates were similar for coast live oaks and black oaks, but considerably greater for tanoaks (table 1). Mortality not attributable to *P. ramorum* serves as an estimate of background mortality. The proportion of the total living trees that were symptomatic, recorded at 1-year increments, increased gradually for coast live oaks and black oaks, whereas tanoaks exhibited a rapid increase from 2000 to a peak in 2004, then declined. This decline is likely a result of decreasing numbers of live stems in these heavily impacted sites.

¹ A version of this paper was presented at the Fourth Sudden Oak Death Science Symposium, June 15-18, 2009, Santa Cruz, California.

² Dept. of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720.

³ USDA Forest Service, Pacific Southwest Research Station, Albany, CA 94710.

⁴ University of California Cooperative Extension, Novato, CA 94947.

⁵ School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931.

⁶ Division of Agriculture and Natural Sciences, University of California, Oakland, CA 94607. Corresponding author: bmcpherson@berkeley.edu.

Table 1—Infection and mortality rates for coast live oak, black oak, and tanoak from 2000 to 2008 (percent y⁻¹)

| Species | Infection | Mortality | Non- <i>P. ramorum</i> Mortality |
|----------------|-----------|-----------|----------------------------------|
| Coast live oak | 5.0 | 3.1 | 0.54 |
| Black oak | 4.1 | 2.4 | -- |
| Tanoak | 10.0 | 5.4 | 0.75 |

We modeled the decreasing numbers of asymptomatic coast live oaks and tanoaks resulting from the disease, using the over-dispersed Poisson regression. A regression line was fitted using the total number of asymptomatic trees from each plot with time as the independent variable, from March, 2000 to March, 2008, with plot nested in site as a random effect to account for the over-dispersion due to the repeated measurements. Asymptomatic coast live oaks were projected to decrease 50 percent by 2012 and 90 percent by 2036. For tanoaks, a 50 percent decrease occurred by 2005, with a 90 percent decrease projected by 2015.

Infection rates increased for all three species as a function of increasing stem DBH. Beetles have been shown to preferentially attack the larger bleeding coast live oaks (McPherson and others 2005). Numbers of attacks increased with increasing canker size (McPherson and others 2008). As a consequence, the mean size of surviving trees has decreased since 2000.

Disease stage-specific mortality was modeled using Cox proportional hazards (PH) analysis and Weibull survival analysis (Lee and Wang 2003). For each species, we modeled the overall survival of all trees that were asymptomatic in 2000. We then applied the analysis to initially asymptomatic cohorts of trees that 1) developed bleeding, and 2) developed bleeding and then were colonized by beetles. Variables included site (CCSP or MMWD), plot, and DBH. Each tree was assessed twice per year, in March and September, from 2000 to 2008.

Survival functions in both models were comparable, with the Weibull curves all lying within the 95 percent confidence intervals of the corresponding Cox PH curves. Median Weibull survival estimates (the point where the probability of surviving longer than a given time is 0.5) for trees that were asymptomatic in 2000 were similar for coast live oaks and black oaks, but less for tanoaks (table 2). For each species, estimates for trees that developed bleeding were 25 percent to 50 percent lower than the overall estimates. Beetle attacks further reduced median survival by 65 percent to 80 percent.

Table 2—Estimated median survival times (years) for initially asymptomatic trees (SE)

| Species | | Overall Asymptomatic | Bleeding | ¹ Bleeding + Beetles |
|----------------|------|----------------------|------------|---------------------------------|
| Coast live oak | CCSP | 15.8 (1.5) | 11.7 (2.7) | 2.4 (0.6); 3.4 (0.8) |
| | MMWD | 11.7 (0.8) | 7.5 (1.6) | 1.9 (0.5); 2.6 (0.5) |
| Black oak | | 13.8 (3.0) | 6.2 (1.3) | 1.9 (0.9) |
| Tanoak | | 8.8 (0.7) | 5.9 (0.7) | 1.7 (0.4) |

¹The two values shown for coast live oaks with bleeding and beetles represent cohorts with mean DBH = 20 cm (upper entry); mean DBH = 40 cm (lower entry).

The survival analyses reported here update earlier Weibull analyses that differed in two respects. In the earlier model, each same-symptom disease status cohort was composed of individuals with the same symptom status in March 2000, and trees were evaluated once per

year (McPherson and others 2005). By 2008, sufficient numbers of trees had progressed from asymptomatic to bleeding and ultimately to death that we could use only asymptomatic trees as the starting cohort. The value of the Weibull modeling approach is evident in the consistency of the estimates derived for symptomatic trees in both the 3- and 8-year time frames. Although the overall survival estimates for coast live oaks probably overestimated median survival times in the earlier model, 29.5 (SE = 8.4) y and 31.8 (9.3) y, survival estimates for bleeding trees were 7.0 (1.2) y and 7.6 (1.6) y, and for beetle-colonized trees, 2.6 (0.3) y and 3.2 (0.6) y, for CCSP and MMWD, respectively (McPherson and others 2005). For tanoaks, the earlier estimate for overall median survival was 12.6 (3.8) y, for bleeding trees, 8.7 (2.3) y, and for beetle-colonized trees, 2.9 (1.0) y. In general, the modeled median survival estimates for symptomatic coast live oaks and tanoaks were more consistent for the two models than were the estimates for overall survival. Once beetles attacked trees, both models showed dramatic, consistent decreases in survival.

Basal area of all woody stems was measured in 2001 and 2007 in 0.08 ha plots sited within the larger plots. Live California bay laurel (*Umbellularia californica*) basal area increased by 8 percent during this period. The proportion of coast live oaks in the disease progression plots that were symptomatic and dead was positively related to bay laurel stand basal area in 2001 ($F_{1, 14} = 13.096$, $P < 0.0028$) and in 2007 ($F_{1, 14} = 4.99$, $P < 0.042$). The diminished strength of the relationship suggests that the role of bay laurel in *P. ramorum* transmission to coast live oaks was more important early in the epidemic and decreased with time. Live Pacific madrone (*Arbutus menziesii*) basal area decreased 12 percent during the same period. There was a negative relationship between madrone basal area and the proportion of coast live oaks that were symptomatic and dead. The strength of this negative relationship increased from 2001 ($F_{1, 14} = 3.41$, $P > 0.086$) to 2007 ($F_{1, 14} = 5.16$, $P < 0.0028$). We also found an inverse relationship between basal area of bay laurel and madrone in these plots. We hypothesize that the contrasting trends of the relationship between basal area of bay laurel and madrone is correlated with moisture availability or with variables dependent on moisture availability, such as the infection process. In these forests Pacific madrone tends to be found in drier sites and bay laurel is more dominant in wetter sites.

This study of the responses of individual host trees supports wider use of survival analysis to model ecological change driven by introduced pathogens. Because relatively few variables are required to develop predictions of change at the stand and landscape scales, survival analysis can serve as a useful tool for land management decisions.

Literature Cited

- Rizzo, D.M. and Garbelotto, M. 2003.** Sudden oak death: endangering California and Oregon forest ecosystems. *Frontiers in Ecology and the Environment*. 1(5): 197–204.
- Lee, E.T. and Wang, J.W. 2003.** *Statistical methods for survival data analysis*. Wiley-Interscience, New York.
- McPherson, B.A.; Wood, D.L.; Storer, A.J.; Svihra, P.; Rizzo, D.M.; Kelly, N.M. and Standiford, R.B. 2000.** Oak mortality syndrome: sudden death of oaks and tanoaks. *Tree Notes*, Number 26, California Department of Forestry and Fire Protection. 6 p.
- McPherson, B.A.; Mori, S.M.; Wood, D.L.; Storer, A.J.; Svihra, P.; Kelly, N.M. and Standiford, R.B. 2005.** Sudden oak death in California: disease progression in oaks and tanoaks. *Forest Ecology and Management*. 213: 71–89.
- McPherson, B.A.; Erbilgin, N.; Wood, D.L.; Svihra, P.; Storer, A.J. and Standiford, R.B. 2008.** Attraction of ambrosia and bark beetles to coast live oaks infected by *Phytophthora ramorum*. *Agricultural and Forest Entomology*. 10: 315–321.