Regeneration of Oaks and Tanoak in *Phytophthora ramorum*-Affected Forests[1]

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Abstract

Recent mortality in coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii*), and tanoak (*Lithocarpus densiflorus*) exceeds historical levels in forests affected by the pathogen *Phytophthora ramorum*. We assessed the balance between recent mortality and seedling populations in these species to examine the status of regeneration in stands with varying levels of mortality caused by *P. ramorum* and other agents. Regeneration data were collected from two sets of permanent 0.02 ha plots. In a set of 150 plots distributed across 12 locations where *P. ramorum* is present, seedling counts and mature tree condition were rated annually from 2000 through 2005. In a second set of 250 plots distributed across 11 locations with and without *P. ramorum* in Sonoma County, data were collected in 2001 and 2004.

Data from plots assessed annually showed that coast live oak seedling populations fluctuated more widely from year to year than did tanoak seedling populations. Across both plot sets, tanoak seedlings were consistently present in plots with tanoak trees. Consequently, nearly all plots with tanoak mortality had tanoak seedlings, which could potentially grow to replace dead trees. Coast live oak seedlings were present in about 80 percent of all plots with coast live oak trees. About 6 to 8 percent of plots with coast live oak trees had mortality but no coast live oak seedlings. Less than half of all plots with California black oak trees had California black oak seedlings. Three-quarters of the plots with California black oak mortality lacked seedlings of this species. In these forests, regeneration of California black oak appears inadequate to maintain stand density even without the additional mortality due to *P. ramorum*.

Keywords: Mortality, Phytophthora ramorum*, regeneration, sudden oak death, SOD.*

Introduction

The exotic pathogen *Phytophthora ramorum* causes bark cankers that can kill mature coast live oak (*Quercus agrifolia*), California black oak, (*Q. kelloggii*), and tanoak (*Lithocarpus densiflorus*) trees. *P. ramorum* canker, also known as sudden oak death (SOD), has recently become a major cause of tree mortality in these three species in a number of California counties (Rizzo and others 2002, Swiecki and Bernhardt 2006). By killing overstory trees of these species, *P. ramorum* canker has the potential to change the composition of infested forests over the short term. Long-term composition changes may result if overstory mortality is not replaced by trees of the same species.

Populations of seedling advance regeneration present in the understory prior to overstory tree mortality play an important role in determining whether canopy gaps created by oak or tanoak mortality will be filled by these same species. Seeding populations can vary over time due to fluctuating rates of establishment and mortality. For example, because acorn production is highly variable from year to year

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(Koenig and Knops 2005), few or no seedlings may become established in years with low acorn production.

P. ramorum is able to cause twig infections in tanoak, but not in coast live oak. Both coast live oak and tanoak seedlings developed cankers when artificially inoculated at a wound with *P. ramorum*, but tanoak developed longer cankers, and only tanoak seedlings were killed (Rizzo and others 2002). Furthermore, *P. ramorum* stem cankers do not typically occur on small-diameter coast live oak, and did not occur in trees with a bark thickness of less than 1 cm (Swiecki and Bernhardt 2005a). Therefore, tanoak appears to be susceptible to *P. ramorum* canker from the seedling stage though the mature tree stage, whereas coast live oak seedlings do not appear to be at risk of *P. ramorum* canker.

We assessed both tree mortality and seedling populations of coast live oak, California black oak, and tanoak in two separate sets of permanent study plots. The first of these studies was initiated in September 2000 as a case-control study of factors affecting disease occurrence and progress in coast live oak and tanoak (Swiecki and Bernhardt 2002, 2005a, 2006). All of these plots were established in areas where SOD was common, and have been re-evaluated annually through 2005 in order to study factors related to disease onset and progression. The second study was designed to assess SOD impacts over time to tree health in Sonoma County woodlands and forests containing these three hardwoods. These plots were established in 2001 and re-evaluated in 2004 (Swiecki and Bernhardt 2005b, these proceedings). This paper reports on seedling population data collected in these two independent studies and on the balance between advance regeneration and overstory mortality.

Methods

Plot selection

Case-control study plots

Case-control study plots were established in September 2000. A total of 150 plots were distributed across 12 study areas located primarily in Marin County (*table 1*). Plots were established in areas where *P. ramorum* had been shown to be prevalent. Study sites were selected on the basis of appropriate vegetation type (adequate representation of coast live oak or tanoak), the presence of cases (trees with symptoms of *P. ramorum* canker) and controls (asymptomatic trees) in the study area, and absence of recent disturbances that might affect tree health (e.g., root-damaging construction). Coast live oak was the subject host species at 10 of the 12 locations; tanoak was the subject species at the remaining two locations (Swiecki and Bernhardt 2002, 2005a).

***Table 1**—Study locations with numbers of plots and host species present at each.*

Location number[1]	Location	Number of plots	Subject tree species
1	Marin Municipal Water District (MMWD) watershed - Azalea Hill area	12	coast live oak
2	MMWD-Pumpkin Ridge south	16	coast live oak
3	MMWD-Pumpkin Ridge north	11	coast live oak
4	MMWD-Phoenix Lake area	11	coast live oak
5	China Camp State Park - Miwok Meadows area	16	coast live oak
6	China Camp State Park - SE Buckeye Point area	12	coast live oak
7	Woodacre (Private land)	12	coast live oak
8	Lucas Valley (Private land)	12	coast live oak
9	Muir Woods NM / Mt. Tamalpias SP	10	tanoak
10	Wall Road (Private land)	13	coast live oak
11	Novato (Private land)	13	coast live oak
12	Jack London State Park	12	tanoak
2-1	Jack London State Park[2]	24	Cal. black oak, tanoak, coast live oak
2-2	Sugarloaf Ridge State Park	25	coast live oak
2-3	Lake Sonoma (Army Corps of Engineers)	24	coast live oak, Cal. black oak
2-4	Weston (private land)	26	coast live oak, Cal. black oak
2-5	Austin Creek State Recreation Area	25	tanoak, Cal. black oak
2-6	Modini (private land)	25	Cal. black oak, coast live oak
2-7	Annadel State Park	24	Cal. black oak
2-8	Salt Point State Park	18	tanoak
2-9	Helen Putnam Regional Park	24	coast live oak, Cal. black oak
2-10	Foothill Regional Park	15	Cal. black oak, coast live oak
2-11	Sonoma Coast State Beach	21	tanoak

[1]Study locations 1 through 12 are from the case-control study, and except for locations 10 (Napa County) and 12 (Sonoma County) are located in Marin County. Locations 2-1 through 2-12 are from the Sonoma County study.
[2]Study locations 12 and 2-1 were in different areas of Jack London State Park, separated by about 1 km and differing in elevation by about 170 m.

At each study location, we established 10 to 16 circular 8 m radius (0.02 ha=0.05 acre) fixed-area plots, each of which was centered at a subject tree. Interplot spacing varied with vegetation and terrain and the distribution of plots across the landscape varied by location. To avoid overlap between plots, no two adjacent plot centers were located closer than 16 m apart; centers of most adjacent plots were separated by 20 to 30 m.

Each tree in each plot was identified by distance and azimuth from the plot center and by DBH. We evaluated the disease status and condition of all coast live oak, California black oak, and tanoak trees (DBH≥3 cm) in the plots every September from 2000 through 2005 (Swiecki and Bernhardt 2002, 2005a). In the initial (2000) evaluation, dead oaks and tanoaks were counted only if it appeared that they had died within the previous 10 years.

At each assessment, the likely cause of recent tree mortality was determined. Confirmation of *P. ramorum* from selected trees was made by culturing tissue pieces on PARP agar media (Swiecki and Bernhardt 2005a).

Seedlings (DBH<3 cm) of coast live oak, California black oak, and tanoak were counted in each plot in September each year using hand tally counters. If live seedlings of any species were too numerous to tally, numbers of seedlings were estimated. For other forest canopy species, seedlings in plots (plants up to 3 cm DBH) were not counted but were noted as present or absent only in 2000.

Sonoma County Study Plots

In 2001, we established 250 plots at 11 locations throughout Sonoma County to monitor forest health and the spread of *P. ramorum* (Swiecki and Bernhardt 2005b, these proceedings). Locations were chosen in areas where tanoak, coast live oak, and/or California black oak were common (*table 1*).

Plots at each location were established at vertices of a grid superimposed over a map of the location and are unbiased with respect to tree condition or the presence or absence of *P. ramorum* canker. The only requirements for establishing a plot at a grid intersection was that coast live oak, California black oak, and/or tanoak were present and the slope was navigable (generally no greater than about 70 percent). Plot selection and placement details are given in Swiecki and Bernhardt (these proceedings).

Plots were the same type as those in the case-control study described above (0.02 ha circular plots) except that plots were centered at random points rather than at trees. The nominal spacing between grid points was 50 m as plotted on a topographic map, with the exception of the first location (Jack London SP) where the grid spacing was 60 m. Because only plots containing coast live oak, California black oak, and/or tanoak were sampled, the pattern of actual plot positions often differs from the idealized sampling grid. In addition, the overall area represented by the sampled plots in each grid varied between locations, from about 4.7 to 14 ha, depending on the distribution of the host trees at each location.

We collected the same data on tree (DBH≥3 cm) disease status and condition and the presence of seedlings in plots as described for the case-control plots above, but plots were evaluated only in the summers of 2001 and 2004. As described above, we isolated from symptomatic coast live oak, California black oak, tanoak, California bay and some other host species to confirm the presence of *P. ramorum* or other *Phytophthora* species within plots.

Data Management and Analysis

Data summaries and analyses were prepared using JMP statistical software version 5.1.2 (SAS Inc., Cary NC). The square root transformation was applied to seedling count data prior to analysis of variance. Tukey-Kramer HSD was used to test for differences between multiple means. Repeated-measures analysis of variance was used to test for factors related to changes in annual seedling counts. Unless otherwise indicated, effects or differences are referred to as significant if $p \leq 0.05$.

Results

Seedling Populations

Coast Live Oak

Among the 10 coast live oak locations in the case-control study in forests affected by *P. ramorum* and monitored every September between 2000 and 2005, seedling numbers fluctuated widely, both among plots at the same location, and within the same plots from year to year (*fig. 1*). In half of the plots, the maximum number of coast live oak seedlings observed in any year was 10 or less, which corresponds to a seedling density of 500 seedlings/ha or less (1 seedling per plot equals 50 seedlings per ha).

The year 2001 marked a peak in seedling numbers (*fig. 1, table 2*). Seven of the 10 locations had peak seedling populations in 2001, the only year in which average seedling counts per plot differed from other years (*table 2*). In locations that showed strong increases in seedling counts in 2001 compared to 2000, the mean number of seedlings per plot has decreased in subsequent years. It appears that this decrease is due to mortality of many of the seedlings established in 2001.

We used a repeated measures analysis of variance of plot seedling counts to determine whether various factors were associated with changes in seedling populations over time. These analyses indicate that seedling counts varied significantly over time and between locations (F test $p<0.0001$ for both factors) and are somewhat negatively correlated with the number of live coast live oak trees in the plot (F test $p=0.0265$). The interaction between location and time was also highly significant (Pillai's Trace, Wilk's Lambda $p<0.0001$). Factors that were not significantly related to seedling population levels included whether coast live oaks with *P. ramorum* canker symptoms were present in the plot, the number of dead coast live oak trees in the plot, overall plot canopy cover, and shrub cover in the plot.

The Sonoma County plots were evaluated in 2001 and 2004. As in the case-control plots, seedling populations were significantly lower in 2004 than they were in 2001 (*tables 2, 3*). We used repeated measures analysis of variance models to test for differences in coast live oak seedling counts for 2001 and 2004 using data from both the Sonoma and case-control plot sets. As was seen in the analysis of the 2000 through 2005 data from the case-control plots, the effects of time (2001 vs. 2004), location, and the time by location interaction were significant in models using all coast live oak plots from both plot sets (F test $p<0.0001$ for all). Plot set (Sonoma vs. case-control) was not significant, indicating that overall coast live oak seedlings densities did not differ significantly between the two sets of plots overall, despite the significant differences between various locations. None of the other factors tested, including the number of live or dead coast live oak trees or the presence of *P. ramorum* canker symptoms in the plot, significantly affected seedling counts.

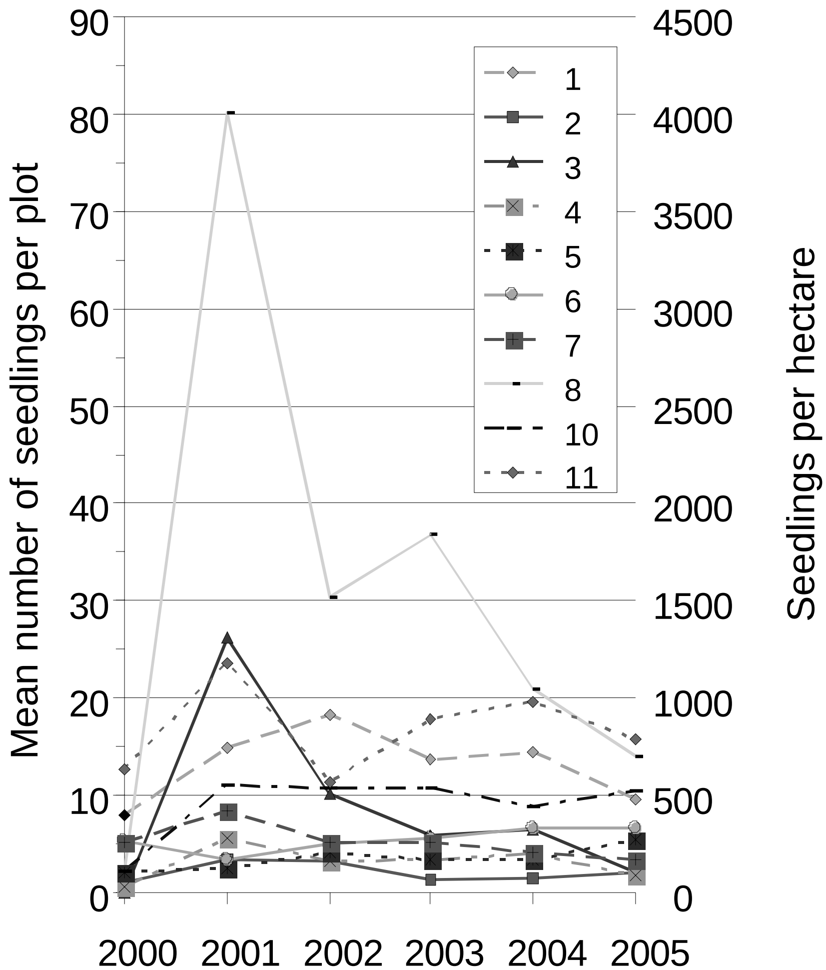

Figure 1—Mean numbers of coast live oak seedlings per plot at each of 10 case-control study locations with coast live oak overstory. Seedling counts were made in September of each year. Location numbers in the legend are the same as in Table 1.

Table 2*—Mean (and standard deviation) of coast live oak seedling or tanoak seedling counts per plot by year in case-control study plots. Coast live oak means are calculated from 125 plots with coast live oak seedlings in at least one year. Tanoak means are calculated from 39 plots that either have tanoak overstory (25 plots) or lacked tanoak overstory but had tanoak seedlings present in at least one year (14 plots).*

Year	2000	2001	2002	2003	2004	2005
Coast live oak	4.0 (5.9)	17.3[1] (32.3)	10 (15.9)	10.2 (20.7)	8.8 (11.4)	7.2 (9.2)
Tanoak	11.8 (13.4)	11.5 (9.5)	13.8 (12.9)	13.1 (13.3)	12.4 (10.3)	13.8 (12.3)

[1] significantly different from means from all other years for this species according to Tukey-Kramer HSD.

Table 3—Mean counts of seedlings (<3 cm DBH) per plot by species in Sonoma County study plots that had seedlings of the species present in 2001 and/or 2004.

Species	Number of plots	2001 mean seedlings/plot (SD)	2004 mean seedlings/plot (SD)
Tanoak	85	22.0 (19.0)	23.1 (20.7)
Coast live oak[1]	119	19.3 (26.9)	11.5[2] (18.1)
California black oak	78	3.7 (8.0)	2.7 (4.1)

[1] Coast live oak means exclude 15 plots with estimated regeneration counts greater than 100 per plot in 2004. Estimated counts in these plots were the same in both 2001 and 2004.
[2] Significantly different from 2001 mean at $p<0.0001$ (two-tailed paired t-test).

The number of dead coast live oak seedlings tallied in the case-control plots each year was almost always much smaller than the drop observed in live seedling numbers from one year to the next. Many small dead seedlings apparently did not persist long enough to be observed in annual evaluations. Presumably, at least some of these may have been destroyed by herbivores. Hence, counts of dead coast live oak seedlings within plots did not provide an accurate picture of seedling mortality from year to year.

California Black Oak

Both overstory trees and seedlings of California black oak were uncommon in the case-control study plots. Counts of black oak seedlings were initiated in 2001, at which time only five plots at four locations had California black oak seedlings present (one to three seedlings per plot). By 2005, only two plots at two locations had California black oak seedlings (one seedling in each plot). These seedlings were not in plots with overstory California black oaks.

In the Sonoma County study, nine locations had California black oak trees. Seedling populations per plot were very low and the average number of seedlings per plot did not change significantly from 2001 to 2004 (*table 3*). Two plots at Weston had an estimated 50 seedlings in 2001, which were reduced to counts of 15 and 2 by 2004. The highest number of California black oak seedlings per plot in 2004 was 24, and only 10 percent of the plots with California black oak regeneration had more than 15 seedlings.

Tanoak

Tanoak twigs are susceptible to *P. ramorum* and understory tanoak seedlings commonly showed tip dieback and/or mortality of individual stems. However, over the period of the case-control study, this damage has not resulted in a reduction in tanoak seedling populations at the three locations that had tanoak seedlings present. According to a repeated measures analysis of variance on the case-control plot data, seedling counts per plot have not changed significantly between 2000 and 2005. The effect of location was significant (F test $p=0.0025$), but the time by location interaction was not significant.

Tanoak seedling counts in the Sonoma County plots showed a similar trend. The average number of seedlings per plot did not change from 2001 to 2004 (*table 3*). Repeated measures analysis of variance models using all tanoak plots from both the case-control and Sonoma data sets for 2001 and 2004 also showed no significant effect of time on tanoak seedling counts. Tanoak seedling counts did differ significantly by location (F test $p<0.0001$), and counts were higher overall in the

Sonoma plots than in the case-control plots (F test p=0.0015). Other factors tested, including the numbers of live or dead tanoak trees or the presence of *P. ramorum* canker symptoms in the plot, were not significantly related to tanoak seedling counts in these models.

Among all plots with tanoak seedlings in both plot sets, the maximum number of seedlings per plot in 2004 was estimated at 100 (5,000 seedlings/ha) and half of the plots had 20 or more seedlings (1,000 seedlings/ha). For the Sonoma plots, tanoaks had the highest and California black oak the lowest seedling counts per plot in 2004, and differences in the average number of seedlings per plot for the three species were significant (Tukey's HSD, p=0.05). However, this result was only obtained if the 15 plots with very high coast live oak seedling counts (150 to 1,000 per plot) were omitted from the analysis (*table 3*). Including these 15 plots gives coast live oak the highest numerical average overall (48 seedlings per plot), but due to the high variance, coast live oak and tanoak seedling counts did not differ significantly from each other.

Distribution of Seedlings Among Plots

Almost all of the case-control study plots with coast live oak overstory had coast live oak seedlings at some point between 2000 and 2005. Only five of these 128 plots had no coast live oak seedlings in any of the six years of the study. However, 46 percent of these plots had no coast live oak seedlings in at least one year. Coast live oak seedlings were also found in plots that lacked coast live oak trees. In 2004, 36 of 156 plots from both plot sets without coast live oak trees had seedlings of this species.

The percent of case-control plots with coast live oak seedlings increased greatly from 2000 to 2001 (*fig. 2*), paralleling the increase in average seedling numbers per plot seen in 2001 (*fig. 1, table 2*). After 2001, the percent of plots with seedlings decreased slightly, but more plots had seedlings in 2005 than in 2000 (*fig. 2*). In the Sonoma plots, the percentage of plots with coast live oak seedlings decreased slightly from 2001 to 2004, and was similar to the percentages from the case-control study for the corresponding years (*fig. 3*).

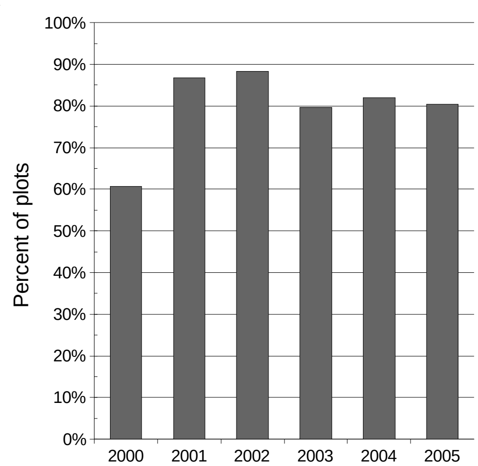

Figure 2—Percent of plots with coast live oak seedlings in September of the year shown.

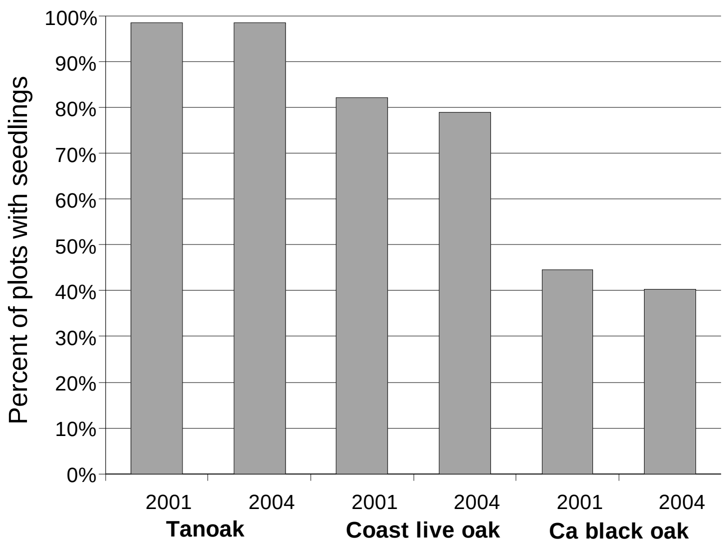

Figure 3—Percent of Sonoma County study plots with regeneration of the same species in 2001 and 2004. Tanoak (73 plots), Coast live oak (114 plots), California black oak (119 plots).

California black oak seedlings were present in less than half of the Sonoma County plots with canopy trees of this species, and the percentage of plots with California black oak seedlings decreased between 2001 and 2004 (*fig. 3*). Hence, California black oak showed both low seedling densities within plots and relatively low constancy within plots with overstory trees. Nonetheless, California black oak seedlings were found in 15 of 270 plots from both plot sets that lacked California black oak canopy.

In contrast, tanoak seedlings were present in almost all plots with tanoak trees. Tanoak seedlings were present in 23 or more of the 25 plots of the case-control plots with tanoak trees between 2000 and 2005. Nearly all of the Sonoma plots with tanoak trees also had tanoak seedlings present in both 2001 and 2004 (*fig. 3*). In 2004, tanoak seedlings were also found in 24 of 302 plots from both sets that had no tanoak canopy.

Seedling Form and Growth

The overwhelming majority of coast live oak seedlings in the plots were very small, typically less than 10 cm tall, and commonly had only one or two stems from the ground. Rarely, very high numbers of these small seedlings were found in plots. Helen Putnam RP was unique in having many plots with very high numbers of seedlings per plot (estimated up to 1,000 per plot). A few larger seedlings, generally up to about 30-cm tall, were found in a few plots at various locations. These larger seedlings were generally multistemmed and shrubby in appearance. In plots that have experienced significant canopy loss due to tree mortality and/or failure over the course of the study, larger shrubby seedlings have become more common, and some of these were up to about 50-cm tall in 2005. Such seedlings are often, but not exclusively, found near or among failed branches and other woody debris that provide some protection from deer browsing. However, none of coast live oak seedlings in either plot set have grown large enough to advance to the tree size class (at least 3 cm DBH).

California black oak seedlings within plots were also typically small (<30 cm) and mostly single-stemmed. We did not observe larger shrubby forms, as seen in coast live oak and tanoak, among California black oak advance regeneration. None of the California black oak seedlings in either plot set has been recruited to the tree stage over the study period.

Tanoak seedlings were normally larger than coast live or California black oak seedlings. Most tanoak seedlings were 30- to 60-cm tall, but some were more than 150-cm tall; smaller seedlings (<30 cm) were also present in some areas. Tanoak advance regeneration most commonly occurred as shrubby seedling-sprouts with multiple stems. Although individual shoots of these seedling-sprouts commonly died back to ground level, we observed relatively few of these larger seedlings that died completely over the course of the two studies. Three tanoak seedlings in the case-control plots, and 14 in the Sonoma plots grew to attain a DBH of 3 cm or more over the respective study periods and are now classified as trees for purposes of data collection.

Balance Between Tree Mortality and Seedling Presence

Coast Live Oak Plots

Plot-level data on tree mortality was compared with seedling counts to provide a measure of the adequacy of advance regeneration. If overstory mortality was present within a plot but understory seedlings of the same species were lacking, we considered that the level of advance regeneration was probably inadequate.

In the case-control plots, the percent of coast live oak plots with at least one dead coast live oak tree nearly doubled between 2000 to 2005 (*fig. 4*). Because the case-control study plots were all in areas affected by *P. ramorum*, 69 percent of the mortality occurring over this interval was due to *P. ramorum*. Over the same interval, the percentage of coast live oak overstory plots with coast live oak seedlings also increased (*fig. 3*). Due to the increase in the number of plots with seedlings, the percentage of plots that had coast live oak overstory mortality but no coast live oak seedlings decreased slightly over this time interval (*fig. 4*). Hence, by this simple metric, it appears that the potential for coast live oak mortality to be replaced though regeneration in these plots has not changed substantially between 2000 and 2005. Although coast live oak seedlings in some plots with recent mortality-related canopy gaps have grown substantially, none of these seedlings have grown large enough to escape browsing of the leader by deer.

In the Sonoma plots, the percent of coast live oak plots with at least one dead coast live oak tree increased between 2001 and 2004 (*fig. 4*). Only four of the nine Sonoma study locations with coast live oak trees also had *P. ramorum* canker present; 39 percent of the coast live oaks that died during this interval were killed by *P. ramorum*. Over the same interval, the percentage of plots with coast live oak seedlings decreased slightly (*fig. 3*). This resulted in a slight increase in the percent of plots with coast live oak overstory mortality but no coast live oak seedlings (*fig. 4*).

California Black Oak Plots

Sixteen California black oak trees were present in 11 of the case-control plots at six locations. Three of these trees died between 2000 and 2005; two of the deaths were due to *P. ramorum*. None of the plots with California black oak trees had California black oak seedlings, so it appears unlikely that California black oak regeneration would replace any of these killed trees.

Among the Sonoma plots, the percentage of plots with California black oak mortality doubled from 2001 to 2004 (*fig. 4*). Five of the nine locations with California black oaks also had *P. ramorum* canker, and 25 percent of the California black oaks that died between 2001 and 2004 were killed by *P. ramorum.* The number of plots with California black oak mortality that lacked seedlings increased three-fold between 2001 and 2004 *(fig. 4*).

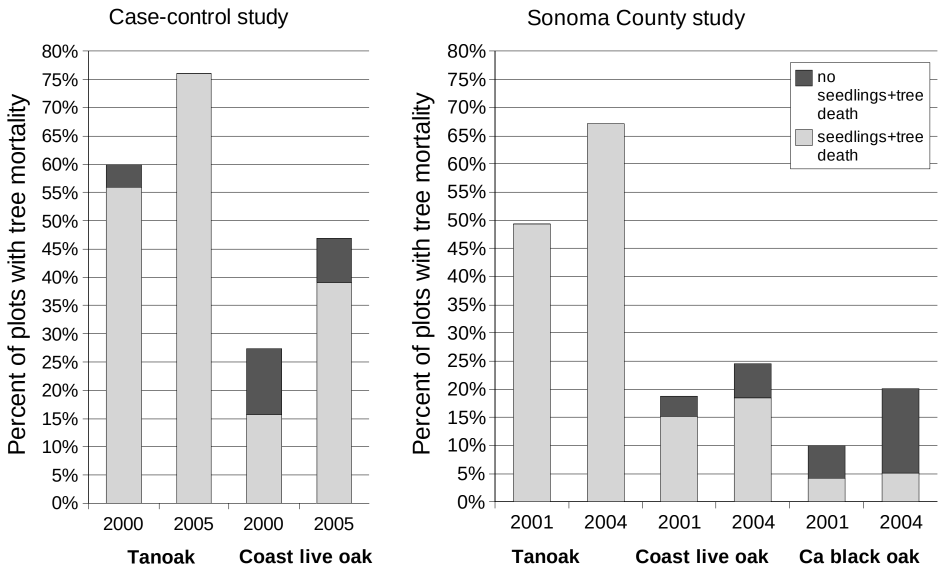

Figure 4—Percent of plots with and without tree mortality and regeneration of the same species in 2001 and 2004. The case-control study includes 28 plots with tanoak and 128 plots with coast live oak trees. The Sonoma County study includes 73 plots with tanoak, 114 plots with coast live oak, and 119 plots with California black oak trees.

Tanoak Plots

Among the case-control study plots with tanoak trees, mortality increased substantially between 2000 and 2005 (*fig. 4*). *P. ramorum* canker, which was present at all locations with tanoaks, killed 76 percent of the tanoaks that died between 2000 and 2005. However, by 2005, all case-control plots with tanoak mortality also had tanoak seedlings (*fig. 4*).

Two of the four Sonoma study locations with tanoak trees were confirmed to have *P. ramorum* canker, but tanoaks at the other two locations are affected by an unidentified canker disease (Swiecki and Bernhardt, these proceedings). The percent of Sonoma plots with mortality of tanoaks increased substantially between 2001 and 2004 (*fig. 5*); 36 percent of the tanoaks that died during the interval had *P. ramorum* canker. All of the plots with dead tanoak trees also had tanoak seedlings in both 2001 and 2004.

Seedlings of Other Tree Species

In the case-control plots, we recorded whether seedlings of other forest canopy species were present in plots in 2000. California bay (*Umbellularia californica*) regeneration was observed in 67 percent of the study plots. The other most commonly observed seedlings were Douglas-fir (*Pseudotsuga menziesii*), in 43 percent of the plots, and madrone (*Arbutus menziesii),* in 16 percent of plots. In the Sonoma plots, seedlings of other forest canopy species in plots were noted as present or absent in both 2001 and 2004, although no significant changes were observed over this interval. California bay seedlings were found in 64 percent of the Sonoma plots. Other canopy species commonly represented as seedlings in the Sonoma plots included Douglas fir (49 percent of plots), madrone (28 percent of plots), coast redwood (*Sequoia sempervirens*) (12 percent of plots), and bigleaf maple (*Acer macrophyllum*) (9 percent of plots). All of these other species are susceptible to foliar or twig blighting caused by *P. ramorum*.

Discussion

Regeneration involves replacement of existing trees that die. For oaks and tanoaks, most of this replacement occurs via persistent seedlings (advance regeneration) that have become established in the understory. These seedlings are typically not released until a gap in the canopy is created or suppressive effects of overstory trees are otherwise reduced.

Tanoak seedlings in both studies were present in a range of size classes, but much of this advanced regeneration consisted of “seedling-sprouts” (Burns and Honkala 1990). These are small, shrubby plants that form from seedlings whose shoots have periodically died back to the ground and been replaced by new shoots arising from the root crown or basal burl. Due to its understory tolerance and growth form, tanoak advance regeneration was consistently larger than coast live oak and California black oak advance regeneration observed in the plots. Overall, it appears that these smaller oak seedlings did not persist in the understory as long as did the larger tanoak seedlings.

Tanoak seedlings also showed better growth in the understory than the oaks. At least 17 of the taller understory tanoak seedlings attained a DBH of 3 cm or more during the course of the two studies. In contrast, no oak seedlings were recruited to the tree stage, and the best growth was seen among coast live oak seedlings that were in recent canopy gaps.

The density of coast live oak seedlings within plots varied much more widely over time than did tanoak or California black oak seedling densities. From the case-control study data, it appears that large numbers of coast live oak seedlings became established in some years, such as in early 2001 (*fig. 1*). This is probably related in part to a good acorn supply in the preceding fall. The fall 2000 acorn crop for coast live oak had the highest counts recorded for the period from 1993 through 2005 in an annual mast survey of California oaks (W. Koenig and J. Knops, unpublished). Many of the new seedlings established after this heavy mast year apparently did not survive for more than one to two years (*fig. 1*). Because mast production for a given oak species is typically similar over a relatively wide geographic area (Koenig and Knops 2005) it is likely that the decline in seedling numbers in 2004 compared to 2001 seen in the Sonoma plots represents the same phenomenon seen in the case-control plots.

The comparison between mortality and seedling presence indicated that coast live oak mortality has the potential to be replaced by regeneration in most of the study plots (*fig. 4, 5*). However, considering the small size and limited persistence of coast live oak advance regeneration, there is no guarantee that sufficient numbers of seedlings present in these plots will survive long enough to be recruited. Coast live oak seedling counts in plots were generally low, averaging less than 10 seedlings per plot in case-control plots and just slightly higher in Sonoma County locations (*tables 2, 3*).

Furthermore, recruitment of coast live oak seedlings appeared to be strongly dependent on canopy gaps. Due to the high stocking levels found in many of the stands, relatively small canopy gaps may be refilled relatively quickly through growth of remaining overstory or understory, possibly inhibiting coast live oak seedling recruitment. Even if canopy gaps are large enough and relatively long-lived, virtually all of the stands we studied also had regeneration of various tree canopy species present. Faster growing species, such as Douglas fir, may overtop and suppress coast live oak regeneration in these gaps, especially at more mesic sites. Hence, it is likely that long-term reductions in coast live oak stand density may occur in more than the 6 to 8 percent of coast live oak plots that have recent coast live oak mortality and lack coast live oak regeneration.

The regeneration data gathered to date indicates that among the SOD canker hosts studied in the Sonoma plots, California black oak populations are currently at greatest risk of decline as the result of non-replaced overstory mortality. The case-control study does not include enough California black oak to draw strong conclusions. However, it is unlikely that California black oaks killed by *P. ramorum* in the case-control plots will be replaced by regeneration of this species. Due to sparse seedling production by California black oak, long-term losses in the density of this species are likely to occur in stands with even low levels of mortality due to *P. ramorum*. Indeed, current levels of advance regeneration in California black oak appear to be inadequate to offset tree mortality due to agents other than *P. ramorum*.

In contrast, the potential for tanoak regeneration currently appears to be quite robust, at least at the locations we studied. Even though tanoak seedlings are susceptible to *P. ramorum* canker, seedling population data collected to date do not indicate that *P. ramorum* has significantly impacted seedling tanoak populations within areas where this pathogen has become established. However, continued long-term monitoring will be needed to determine whether tanoak seedlings will be able to recruit to the tree size class in areas with high levels of *P. ramorum* inoculum. Although we have seen some tanoak seedlings grow to attain diameters of 3 cm or more over the study period, tanoak stems in this diameter class are susceptible to *P. ramorum* (Rizzo and others 2002) and may be killed before they attain reproductive age. Ultimately, the ability of tanoak to regenerate in areas affected by *P. ramorum* may depend on the prevalence of resistant genotypes within the pool of advance regeneration.

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