Relationships Between *Phytophthora ramorum* Canker (Sudden Oak Death) and Failure Potential in Coast Live Oak [1]

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Abstract

In autumn 2002, we conducted a retrospective study on coast live oak (*Quercus agrifolia*) failures in Marin County, California, woodlands affected by *Phytophthora ramorum* canker (sudden oak death). The objectives of this case-control study were to quantify levels of bole, large branch, and root failure in these woodlands and determine how various tree and stand factors are related to failure potential. Non-failed trees were used as a control population to identify factors that might contribute to tree failure. Rates of bole and large branch (more than 20 cm diameter) failures were significantly higher between about July 2001 and December 2002 than in the period from 1992 through July 2001. Bole failures were the most common type of failure. Based on the estimated date of failure, for the years 1992 through 1996, boles failures occurred in 0.5 percent of the trees each year. The incidence of bole failures increased to 5 percent per year between mid-2001 and the end of 2002. Among recent failures (2001-2002), 39 percent of the bole failures and 30 percent of the scaffold (primary branches arising from the main stem) failures occurred in live stems. Most root and root crown failures also occurred in live trees. Among trees with recent failures (2001-2002), 83 percent showed symptoms of *P. ramorum* canker. Branch, scaffold, and bole failures were strongly associated with advanced symptoms of *P. ramorum* canker, which include evidence of wood degradation by *Hypoxylon thouarsianum* and/or various wood boring beetles.

Early *P. ramorum* canker symptoms, consisting of only bleeding cankers without secondary invasion, were not associated with an increased likelihood of failure. Wood decay was the most consistent and important factor influencing failure potential. Decay was present and rated as a contributing factor in almost all failures. Fruiting bodies of *H. thouarsianum* and

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other wood decay fungi, decay columns, and canker rot symptoms were significantly more common among failures than among non-failed controls. Several variables indicative of wood decay were highly significant predictors of failure in both recursive partition and multivariate logistic regression models. Beetle boring was also significantly more common among failures than among non-failed trees. Other factors associated with increased failure potential include overtopping of the tree by other trees, local alteration of the stand canopy due to dead or failed trees, multiple trunks, multiple branches arising from the same point, and asymmetric canopy shape. Failures in both live and dead trees were largely influenced by the same factors.

Key words: tree failure, wood decay fungi, *Hypoxylon thouarsianum,* ambrosia beetles

Introduction

Phytophthora ramorum, the causal agent of sudden oak death, causes bleeding bark cankers on the main stems of tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii*), and several other oak species in California (Garbelotto and others 2001). The bark cankers can expand over time and eventually girdle susceptible trees. The sapwood-decaying fungus *Hypoxylon thouarsianum*, ambrosia beetles (*Monarthrum* spp.), and oak bark beetles (*Pseudopityophthorus* spp.) are commonly associated with *P. ramorum*-infected trees in later stages of decline (Garbelotto and others 2001). These agents also attack declining trees or branches that are not infected with *P. ramorum*.

Prior to this study, there were anecdotal reports that trees infected with *P. ramorum* were more likely to fail than noninfected trees. Because *P. ramorum* cankers primarily affect the bark, cambium, and occasionally some of the outer sapwood (Rizzo and others 2002), it appeared unlikely that *P. ramorum* alone would increase the failure potential of infected trees. Preliminary data released by the University of California, Richmond, Forest Products Laboratory (Shelly 2002) indicated that *P. ramorum* does not directly cause significant losses in wood density of tanoak.

However, wood decay fungi that are associated with *P. ramorum* cankers, such as *H. thouarsianum,* do significantly reduce wood density and strength. Increased levels of wood decay associated with *P. ramorum* cankers could therefore increase the likelihood of failure in trees with sudden oak death. In addition, wood boring beetles, especially ambrosia beetles, are often associated with decay in trees with *P. ramorum* canker. Previous studies had not addressed whether beetle boring contributes meaningfully to failure potential.

To investigate the relationship between sudden oak death and tree failure, we conducted a retrospective study on tree failure in coast live oak woodlands affected by *P. ramorum.* Our objectives were to quantify levels of failure in these stands and determine how various tree and stand factors were related to failure potential. Factors under study included *P. ramorum* canker symptoms, colonization by *H. thouarsianum* and other decay fungi, beetle boring, tree defects, and stand characteristics.

Methods

Study site selection

To observe adequate numbers of both failed trees and trees with *P. ramorum* symptoms, we selected six coast live oak stands in Marin County, California, in which both conditions were common. The stands used in this study included permanent sudden oak death research plots we had established in September 2000 as part of a related study (Swiecki and Bernhardt 2001, 2002a,b, 2005). We had visited these stands annually beginning in September 2000 and already had observations on overall disease levels and the timing of some recent failures. The study areas all had relatively dense mixed hardwood forests dominated by coast live oak and California bay (*Umbellularia californica*), with lesser amounts of California black oak and madrone (*Arbutus menziesii*). The study area elevations ranged from 30 to 180 m.

Survey design

At each location we surveyed a wide area around the pre-existing plots from the related (Swiecki and Bernhardt 2001, 2002a,b, 2005) study. Field data were collected over a period of about six weeks, beginning in late October 2002. Final observations were made at all locations in December 2002. Boundaries of the surveyed areas were determined from aerial imagery of the sites and readings from a GPS receiver (Garmin® GPS76 used with an external, boom-mounted antenna). Surveyed areas at the six locations ranged in size from 0.95 to 2.08 ha , based on polygons of the study sites created with ArcView® GIS software.

Branch failures were counted only if they were at least 20 cm diameter at the point of failure. Bole, root crown, and root failures were counted if they affected main stems at least 15 cm diameter at 137 cm height (DBH). Within each of the study areas, we catalogued all failures of coast live oak and California black oak that exceeded these minimum size thresholds and appeared to have occurred within the past 10 years. We recorded GPS coordinates of trees with rated failures. Seven of the failures (2.3 percent) were secondary failures, i.e., failures that occurred because the trees were hit by material from an adjacent tree failure. These failures were excluded from the study results.

We used a case-control study design to investigate relationships between various tree and plot factors and failure potential. Cases were 106 coast live oak trees with recent failures (occurring within about 1.5 years of the survey date) that exceeded the minimum size thresholds noted above. Cases were selected randomly from observed recent failures, and were spatially stratified to ensure that cases were distributed throughout the study areas to the degree possible. The number of cases rated per location ranged from 11 to 25.

Controls were 170 non-failed coast live oaks within the sampled stands where the failures were located. The number of controls rated per location ranged from 22 to 37. We sampled both near controls, i.e., the nonfailed tree closest to a given failure, and far controls, i.e., non-failed trees located away from failures. Overall, 103 controls were located within 10 m of a failed tree and 71 were more than 10 m from a failure. Far controls were included to ensure that variation in site factors (e.g., slope, aspect) was not constrained, since such factors tend to be similar among trees that are near each other. Both types of controls were sampled without bias and were not matched to cases with respect to tree form or other characteristics. This allowed us to investigate a wide variety of tree and site factors as potential explanatory variables in the statistical models.

After cataloging all failures, we made a complete count of all coast live oak and California black oak trees with DBH of 10 cm or more within each study area.

Variables assessed

For all failed trees within the study areas, we recorded various characteristics of the failures, including: site of failure (bole, branch, etc.); diameter at the point of failure, major factors contributing to the failure (decay, cavity, beetle boring, structural defects, wounds). We estimated the failure date using a variety of indicators including the amount of oxidation and weathering of the broken wood surface, the condition of foliage, if any, degradation and loss of fine twigs, the amount and type of debris that had accumulated on exposed surfaces, and knowledge of recent failure dates based on previous visits to the sites. Failure dates were assigned to one of the following time classes: (1) July 2002 to December 2002; (2) January to June 2002; (3) July to December 2001; (4) before July 2001 but within the previous 5 years; (5)

between 5 and 10 years ago. The first three time intervals were subsequently combined to form the recent failure age class (i.e., within 1.5 years of the survey).

The data listed above were collected for failures in 141 coast live oaks and 13 California black oaks that were not used as cases. In addition, for a small number of failed trees (24 coast live oaks and five California black oaks), factors contributing to failure were not rated. These were older (failed more than 1.5 years before the survey) and/or relatively small-diameter failures that were not observed until the complete count of trees within the study locations was conducted in December 2002. These 29 trees are included in overall failure percentages but are excluded from some analyses.

For recent failures (failed within 1.5 years of the survey) that were assigned as cases, we assessed the above variables and a number of additional variables related to the failure. These included whether the failure was associated with previous failures; thickness of failed wood; failure direction; height of failure above the ground; depth of beetle boring; and number of induced (secondary) failures. We also determined the status of the failed part at the time of failure (live or dead). Status was generally obvious for very recent failures. For somewhat older failures, we inferred the status at the time of failure from factors such as the degree of leaf retention and orientation of dead leaves, evidence of post-failure wilting of leaves and stems, moisture level in the wood, the pattern of breakage on impact, and sunburning of bark on large stems, which commonly occurs after failures of live stems.

For all cases and controls, we also collected a wide variety of data on tree form, condition, and site characteristics. These included ground slope and aspect; canopy exposure to overhead light and to wind from the side; presence of recent changes in stand density around the subject tree; number and diameters of stems over 3 cm DBH; presence and severity of symptoms related to *P. ramorum* canker, including the extent of beetle boring damage and *H. thouarsianum* sporulation; the presence, type, extent, and location of decay and cavities; type(s) fungal fruiting bodies present; overall tree condition, and the presence of a variety of structural defects that may contribute to failure. Tree defects rated included those used in the California Tree Failure Report Program (CTFRP) rating form (Edberg and others 1993). A complete description of all variables assessed in failed trees and controls is reported in Swiecki and Bernhardt (2003).

Evaluations of *P. ramorum* canker on case and control trees were based on visual symptoms, including external bleeding and discolored bark tissue visible when the outer bark surface is sliced away (Rizzo and others 2002). For 51 trees failed and control trees in this study that were also located within the pre-existing plots from our other study, disease evaluations had been made in September 2000 and 2001 as well as in the year of the survey. *P. ramorum* has been isolated from symptomatic trees at all of the study locations by ourselves and/or other researchers. However, because isolation efficiency would likely have been low due to both the time of year that trees were evaluated and the fact that many of the failed trees were already dead, we did not attempt to isolate *P. ramorum* from symptomatic trees in this study.

Statistical analyses

We used JMP® statistical software (SAS® Inc., Cary NC) for data analysis. Unless otherwise indicated, effects or differences are referred to as significant if $p \leq 0.05$. Only one failure per tree was used for all statistical model building. For the few case trees in which more than one failure was scored, one failure was randomly selected to be included in the recursive partition and logistic regression analyses.

We used the likelihood ratio chi square statistic to test for independence of variables in 2×2 or larger contingency tables. We used the recursive partitioning platform in JMP® to develop models relating various predictor variables to the case (failure) outcome. The platform recursively partitions data in a dichotomous fashion according to a relationship between the predictor and outcome values, creating a tree of partitions. Each partition is chosen to maximize the difference in the responses between the two branches of the split. Splitting was done interactively and was stopped when an endpoint had fewer than five trees in it or consisted of all failures or controls. After splitting, models were pruned upward to minimize the misclassification rate. We also calculated and compared k-fold crossvalidated G^2 statistics (k=5) for candidate models to assess relative improvement in fit when building models. Unless they were associated with a large change in the crossvalidated G^2, we also pruned splits in which both sides of the split had a majority of the same outcome (cases or controls).

For logistic regression models of the case (failed) versus control (not failed) outcomes, the likelihood ratio chi square was used to test the significance of each effect in the model. We also calculated Akaike's information criterion (AIC) to compare the fit of alternative models. For models constructed for a given data set, smaller AIC values indicate better model fit.

Results

Overall failure rates

Within the six study areas, we recorded data on 1540 coast live oak and California black oak trees (*table 1*). We catalogued 308 failures that were within the age range (past 10 years) and size classes (at least 20 cm diameter for branch failures, at least 15 cm diameter for bole or root failures) that were used as cutoffs for the study. The catalogued failures occurred in 297 trees, some of which had multiple large failures. An additional 105 failures slightly below the size thresholds were observed in the study areas. With one exception (a bole failure less than 15 cm diameter), these were branches that were between 10 and 20 cm in diameter. Trees with these smaller failures are not included in the analyses of failures discussed below.

Table 1— *Coast live oak and California black oak failures by type and study site characteristics at the six study locations.*

Location	Area[1] (ha)	Total trees surveyed[2]	Percent of trees with failures	Percent bole failures[3]	Percent branch failures[3]	Percent root and root crown failures[3]
2	1.984	489	8	70.5	25.0	4.5
3	1.494	286	20	62.5	28.6	8.9
5	2.077	204	23	37.2	51.0	11.8
6	1.471	186	31	67.3	22.4	10.3
8	1.668	163	33	35.8	49.1	15.1
11	0.949	212	20	41.3	56.5	2.2
Totals	9.644	1540	19	52.6	38.3	9.1

[1] Areas are based on flat GIS polygons and underestimate actual surface area due to significant ground slopes at many sites.
[2] Includes only coast live oak and California black oak trees within surveyed areas.
[3] Percent of all failures occurring within the previous 10 years that were above the following size thresholds: branch failures greater than 20 cm diameter, bole, root, and root crown failures of stems greater than 15 cm DBH.

The percentage of failed trees differed significantly between the six locations (likelihood ratio test $p<0.0001$) and ranged from 8 percent to 33 percent. The relative prevalence of bole, branch, and root failures also varied significantly by location overall (likelihood ratio test $p=0.0001$). The majority of the failures within the target size and age ranges were bole failures (*table 1*).

California black oak was a minor component of the woodlands in the study, comprising only 5 percent of the oak trees included in the sample. Of all trees with failures, 6.8 percent were California black oak. Overall failure rates for coast live oak (19.1 percent) and California black oak (23.7 percent) were not significantly different.

Failure dates

Several types of failures were much more common in the 1.5 years before our survey than in the preceding decade (*fig. 1*). Bole failures showed the greatest rate of increase overall, but the rate of branch failures also changed significantly over time (likelihood ratio test $p<0.0001$). Root and root crown failure rates did not differ significantly over the three time intervals. None of the study areas had burned in the 10 years prior to the survey and were not subject to other factors that would remove evidence of older failures. Recent failures (within 1.5 years of survey) were common at all study sites, constituting between 45 percent and 74 percent of the observed failures at the different sites.

About one third of the failures that occurred in 2002 apparently occurred in the first half of the year, although the precise timing of these failures could not be determined. However, of 112 recent failures observed, 27 still had green leaves and moist wood, indicating that these failures had occurred within a month or less of the survey. At least six trees failed between successive visits to a site during autumn 2002. We also heard six nearby tree failures between September and December 2002, all of which occurred during calm weather. Our observations indicate that recent failures in the study areas had occurred throughout the year and many occurred in the absence of severe weather during summer and fall 2002.

Condition of failed treesP. ramorum symptoms

In general, the presence of characteristic *P. ramorum* disease symptoms in failed trees could be rated with confidence only for trees that had failed in the previous 1.5 years, so the analysis in this section is restricted to that subset of trees (*fig. 2*). We also scored trees with less definitive *P. ramorum* symptoms as questionable when noting their most likely disease status. Trees with questionable *P. ramorum* disease symptoms are excluded from *fig. 2*, although the overall trends do not change if the questionable trees are included with their most likely disease categories. Trees with *P. ramorum* symptoms failed at a significantly higher rate (likelihood ratio test $p<0.0001$) than trees lacking *P. ramorum* symptoms. Trees with symptoms of *P.*

ramorum canker constituted 83 percent of the trees with failures but only about 31 percent of the non-failed control trees.

The overwhelming majority of recent failures occurred in trees that had *P. ramorum* symptoms and were either dead or had late symptoms of disease, i.e., beetle boring and/or *H. thouarsianum* fruiting bodies present (*fig. 2*). None of the recorded recent failures occurred in trees displaying only early *P. ramorum* canker symptoms, i.e., bleeding cankers only (*fig. 2*). This result indicates that increased risk of failure is associated with degradation of wood by decay fungi and/or beetles following the appearance of *P. ramorum* canker symptoms, not with *P. ramorum* cankers alone.

Most of the recently failed trees that lacked *P. ramorum* canker symptoms were either dead or in decline due to other disease agents (*fig. 2*), most commonly canker rots or other wood decay fungi. Trees killed by these decay fungi usually experienced multiple failures before they died. Among trees without *P. ramorum* symptoms, the proportion of dead and declining trees was significantly greater among cases than among controls (likelihood ratio test $p<0.0001$). Of the 29 recently failed trees without *P. ramorum* canker symptoms, 41 percent were in decline and 34 percent were dead due to other agents. In comparison, among the 113 non-failed controls without *P. ramorum* symptoms, 11 percent were in decline and none were dead. Only a small percentage of non-declining live trees exhibited recent failures above the size thresholds (*fig. 2*).

Bole failures in trees with *P. ramorum* symptoms occurred across the full range of size classes represented in the population (median diameter at failure 37 cm; mean 38.7 cm, standard deviation [sd] 16.7), with the majority of bole failures occurring in trees between 20 and 60 cm diameter at the point of failure. In contrast, most bole failures in trees lacking *P. ramorum* symptoms occurred in stems less than 25 cm (median diameter at failure 23.5 cm; mean 28.4 cm, sd 14.7). These small diameter trees with bole failures were typically suppressed understory trees that were colonized by wood decay fungi.

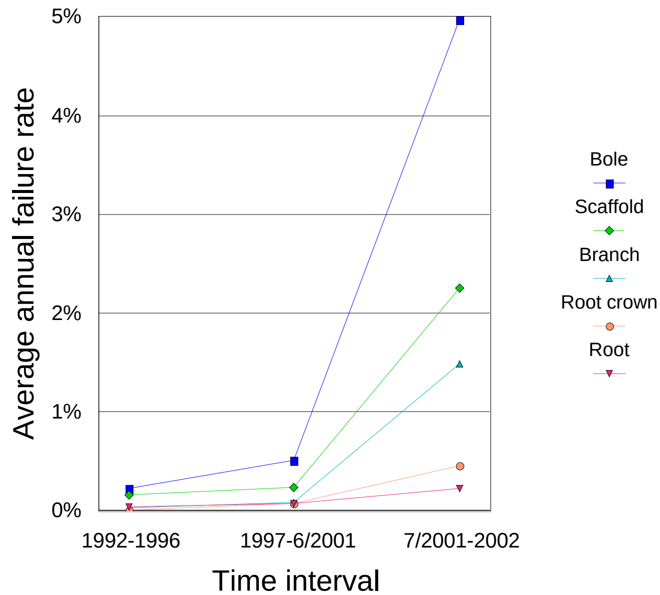

Figure 1—Estimated annual failure rates by failure type for the standing tree population of coast live oak and California black oak within the study areas over three time intervals. The base tree population size was adjusted downward for each interval by subtracting trees with bole, root crown, and root failures that occurred in the previous interval(s) (n=1540, 1521, and 1476, respectively, for the three intervals).

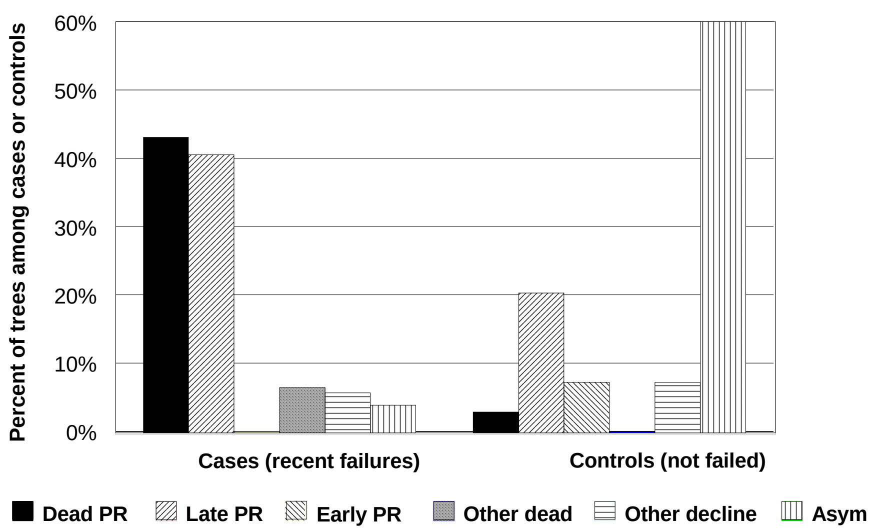

Figure 2— Disease status for coast live oaks with recent (within previous 1.5 years) failures and nonfailed control coast live oaks. Failures and controls with uncertain *P. ramorum* symptoms are excluded; missing columns indicate 0 percent. **Dead PR**= dead trees with extensive *P. ramorum* symptoms; **Late PR**= live trees with *P. ramorum* canker symptoms plus beetle boring and /or *H. thouarsianum* fruiting bodies; **Early PR**= live trees with *P. ramorum* canker symptoms but no secondary organisms; **Other dead**= dead trees lacking *P. ramorum* symptoms, mortality due to other agents; **Other decline**= live trees lacking *P. ramorum* symptoms, in severe decline due to other agents; **Asym**= no evident symptoms of either *P. ramorum* canker or decline due to other agents (n=155 failures and 162 controls).

Most trees with failures were either dead at the time of failure or the failed part was dead at the time of failure. This includes dead main stems of multi-stemmed trees that were classified as having late *P. ramorum* symptoms because they still had one or more live stems. Within the study areas, 75 percent (131/174) of the dead trees had failures above the threshold size. However, a substantial number of live stems also failed. More than 28 percent of all failures occurred in live stems among trees for which the status (living or dead) at the time of failure could be determined (primarily failures occurring within the past 1.5 years). Live stem failures constituted 39 percent of the bole failures and 30 percent of the scaffold (primary branches arising from the main stem) failures. Root and root crown failures also occurred predominantly in live trees.

Factors associated with tree failure

For most failures, we noted the major factors that appeared to have contributed to failure (*fig. 3*). These data do not include older failures for which contributing factors could not be reliably identified. Factors were scored as contributing to failure only if present at levels that were high enough to feasibly affect failure potential. Wood decay was evident in the broken wood surface of almost every failure and was judged to be a major factor contributing to failure in over 96 percent of the observed failures (*fig. 3*). Cavities, beetle boring, and structural problems also contributed to failure in a sizeable number of trees, but in all of these trees, decay was also scored as a contributing factor. For many trees, multiple factors were scored as contributing to failure. Wounds contributed to failure in only a single tree.

In addition to these general ratings, we also made detailed observations on decay, cavities, beetle boring, structural defects, and other factors that might be related to failure potential in case and control trees. We used these and other factors in the statistical models described below to determine which factors were related to failure risk.

Wood decay and cavities

For case trees, we estimated the percent of the stem cross-sectional area at the point of failure that was affected by decay or cavities. Most failed stems showed high levels of decay (*fig. 4*). Cavities were present in only 27 percent of the failures, and only 9 percent had cavities affecting more than half of the cross sectional area (*fig. 4*).

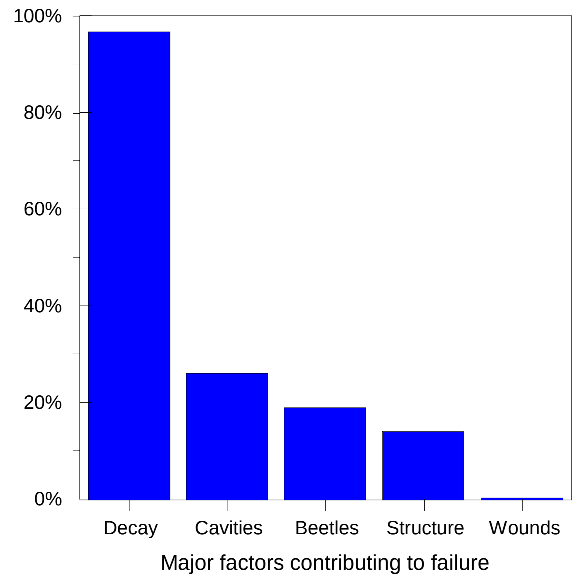

Figure 3— Frequency of major factors contributing to failures (n = 259 failed coast live oak and 13 failed California black oak).

Estimates of decay in non-failed control trees were based on external symptoms only. Although the amount of decay present in controls was probably underestimated, 58 percent of the controls had no obvious decay and only 1 percent of the controls had more than 50 percent cross-sectional decay. These observations suggest that severe wood decay was much less common in non-failed trees than in failed trees.

We probed exposed cavities in non-failed trees to gauge their extent, so cavity ratings of controls are more directly comparable to cavity ratings in cases, at least for open cavities. The distribution of cavity ratings (recoded to three levels for contingency table analysis) did not differ significantly between cases and controls (likelihood ratio test p=0.129). Most observed cavities in both cases and controls were small, and such small cavities did not appear to greatly increase the likelihood of failure in coast live oak.

Cavities and related defects, such as wounds from previous failures and decayed branch stubs, were not consistently present at the point of failure, but 64 percent of the recorded failures were near previous branch or stem failures. The distance between the defect and the point of failure averaged 0.42 m (range 0 to 2 m). When such defects occurred at or very near to the point of failure, they commonly represented a point of structural weakness that contributed to the failure. In other situations, especially where the defects were further from the point of failure, the defects were areas where decay organisms had gained entry into the tree or indicators of decay columns that contributed to both recent and earlier failures on the same stem.

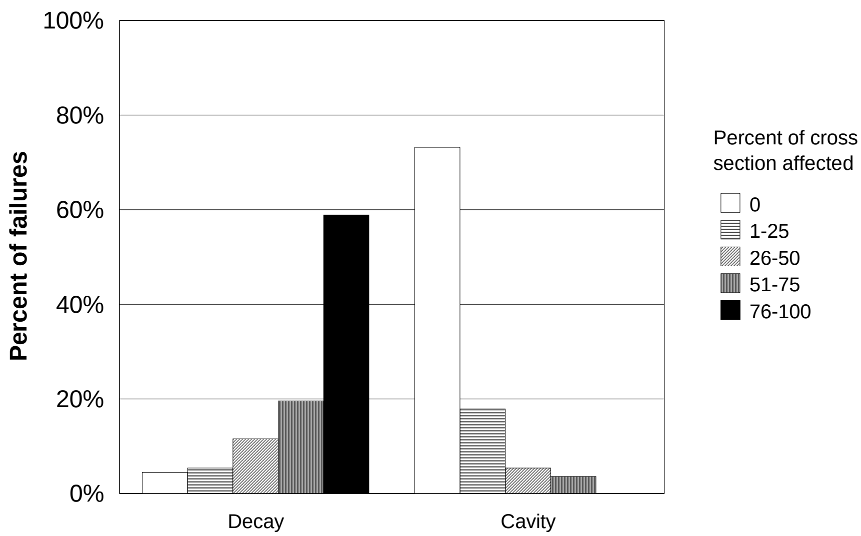

Figure 4—Percent of cross-sectional area at the point of failure affected by decay and cavities among failures scored in coast live oak case trees.

Trees affected by *P ramorum* canker commonly showed fruiting of the wood decay fungus *H. thouarsianum. H. thouarsianum* fruiting bodies (stromata) were present on 91 percent of the cases that had *P. ramorum* canker symptoms, but on only 39 percent of cases without *P ramorum* symptoms. *H. thouarsianum* stromata were present on 82 percent of all case trees but only 21 percent of non-failed control trees (likelihood ratio test $p<0.0001$).

For both cases and controls, we attempted to quantify *H. thouarsianum* infections based on the distribution and density of stromata to determine whether such variables could be used to estimate failure potential. Among all trees, the average rating for the percent of stem circumference with *H. thouarsianum* stromata was significantly higher in cases than controls (t-test $p<0.0001$). To more rigorously test whether distribution of stromata was a predictor of failure potential, we repeated the analysis after excluding trees without *H. thouarsianum* from the analysis. For the 128 trees with *H. thouarsianum* stromata, the percentage of stem circumference with stromata was a significant predictor of failure (likelihood ratio test $p=0.001$). Although the likelihood of failure increased as the percent of the circumference with *H. thouarsianum* stromata increased, the density of *H. thouarsianum* stromata on the stem was not a significantly predictor of failure.

Other decay fungi were also significantly associated with failure risk. The incidence of canker rot symptoms was higher among cases (64 percent) than controls (31 percent) (likelihood ratio test $p<0.0001$). Fruiting bodies of the canker rot fungus *Inonotus andersonii* and *Phellinus* spp., most commonly *P. gilvus,* were also significantly more common among cases than controls. Fruiting bodies of *I.*

andersonii were found only on failed trees. *P. gilvus* often seemed to fill a niche similar to that of *H. thouarsianum* as an opportunistic but somewhat aggressive colonizer of stem areas affected by *P. ramorum* canker.

Beetle boring

Boring by beetles, particularly ambrosia beetles, was significantly more common in cases than controls (likelihood ratio test $p<0.0001$). Among cases, the incidence of beetle boring was 86 percent. In comparison, beetle boring was noted on the lower 2 m of the main stem(s) in 30 percent of controls. Ambrosia beetles were associated with 79 percent of the failures in case trees, although they were frequently not present at levels that were likely to contribute to failure potential (*fig. 3*).

Ambrosia beetle boring was also closely associated with advanced *P. ramorum* canker symptoms. Obvious *P. ramorum* canker symptoms were present in 88.5 percent of the 122 trees (cases +controls) that had evidence of ambrosia beetle boring. Only four trees with ambrosia beetles were rated as free of *P. ramorum* symptoms; the remaining ten were of uncertain disease status.

In failed trees, ambrosia beetle boring was almost exclusively limited to portions of the wood that showed incipient to advanced decay. All of the cases that had beetle boring present also had wood decay present. In contrast, of the failures that had wood decay, 17.8 percent had no ambrosia beetles and 11.6 percent had no evident beetle boring of any type.

We measured the maximum depth to which beetle tunnels extended into the wood on 92 failed stems. The maximum observed depth was 15 cm from the cambium. Thus, beetle boring can potentially reach the center of stems with a below-bark diameter of 30 cm or less. However, the mean depth of boring was 7.3 cm and 90 percent of all ambrosia beetle tunnels extended 10 cm or less into the wood. Depth of boring was not significantly correlated with stem diameter, so as the diameter of the failed wood increased, the proportion of the cross section mined by beetles decreased. Consequently, beetle boring was less likely to directly contribute substantially to loss of wood strength and failure potential in large diameter stems than in small diameter stems.

Structural defects

We scored all cases and controls for the presence of the structural defects listed on the CTFRP tree failure assessment form (Edberg and others 1993) and several other common defects. For failed trees, we also noted whether any of the observed defects were likely to have contributed to the failure.

Overall, many defects were equally common in cases and controls, but several defects were noted more frequently in trees with failures than in non-failed trees (*table 2*). These included decay columns, cavities, one sidedness, and cracks or splits. Although tree structure was scored as a main causative factor in only 20 percent of all failures (*fig. 3)*, structural defects were commonly scored as playing a contributing role in failures (*table 2*). For instance, as noted earlier, many failures occurred in close proximity to defects such as cavities and decayed branch stubs. In such situations, these defects may have contributed to failure potential even though they were not the primary cause of failure. In general, structural defects did not substantially increase failure potential in trees that had little or no decay. However, in trees with substantial amounts of decay, failures were more apt to occur in stems that were also compromised by structural defects.

Only one defect, excessive tree lean, was scored as being present at a significantly higher incidence in controls than in cases. However, we believe that this may be an artifact associated with rating failed trees. Particularly for bole and root crown failures, it can be difficult to estimate the pre-failure amount of lean after failure has occurred.

We coded multiple trunks and co-dominant stems as a single defect type to maintain consistency with the CTFRP reporting form. As shown in *table 2*, the incidence of this combined defect category did not differ significantly between cases and controls. However, stem count data show that 44 percent of trees in this category have a single bole but co-dominant leaders. If trees with multiple stems were considered separately, the percentage of multi-stemmed trees was significantly greater among cases (41 percent) than controls (28 percent) (likelihood ratio test $p=0.035$). In addition, stem count was recorded for all trees within the study areas during the tree count. Using coast live oak data from the entire study area ($n=1431$, excluding secondary failures), bole and root crown failures were significantly more likely to occur in multi-stemmed trees than in single stemmed trees (likelihood ratio test $p<0.0001$ and $p=0.0002$, respectively). The incidence of branch and root failures did not differ between single stem and multi-stemmed trees. In the study areas, most coast live oaks with multiple stems originated from coppice sprouting. Many of these sprout-origin trees have unbalanced canopies and defects at the base of the tree, such as cavities and decay, which may make them more prone to bole and root crown failure.

Table 2— *Frequencies of common structural defects in coast live oak cases (failed trees) and controls (nonfailed trees)*

Defect	Frequency in controls (percent)	Frequency in cases (percent)	Significance[1]	Contributed to failure[2] (percent of cases)
Canopy one sided	58	78	0.0003	94
Multiple trunks/ codominant stems	58	62	ns	35
Hollow branch stubs	53	58	ns	48
Excessive lean	52	27	<0.0001	83
Crook or sweep in bole	50	43	ns	80
Decay column	39	84	<0.0001	84
Embedded bark in crotch	25	15	ns	63
Multiple branches arising at one point	24	30	ns	63
Heavy lateral limb	19	16	ns	82
Cavities	16	38	<0.0001	73
Canopy top heavy	6	8	ns	100
Cracks or splits	2	13	0.0004	86

[1] Significance level of likelihood ratio test comparing frequency of the defect in the controls with that in the cases
[2] For cases only, all defects present were also evaluated as to whether may have contributed to the observed failure.

Multivariate models of factors associated with failure

We developed two types of multivariate models, recursive partition and logistic regression models, to identify factors associated with failure. Both types of models can be used to identify variables that predict an outcome, e.g., the case (failure) outcome in our case-control study. The two types of models are constructed in different ways and can therefore produce somewhat different sets of significant factors. Recursive partition models (other names for the overall technique include decision trees, CART™, etc.) are developed in a sequential, dichotomous fashion. At each step in the analysis, the procedure selects the explanatory factor that maximizes the difference in the responses between the two branches of the split. Subsequent splitting of the partitions is made in the same fashion. In recursive partition models, the algorithm accounts for the possibility that a predictor variable may affect the outcome differently in the presence or absence of another factor, or that the effects of one predictor variable depend on the levels of another. In logistic regression models, such relationships need to be modeled using interactions.

Given the wide variety of variables measured and the fact that some of these variables are highly correlated with each other, the data can be fitted to a number of alternative models. Our objective in constructing models was to explore the relationships between explanatory variables and determine which variables or sets of related variables could be used to identify trees that are most likely to fail.

Recursive partition models

We constructed the recursive partition model for the case outcome (all failure types) starting with 43 possible predictor variables. Candidate predictor variables included defect types, indicators of disease status, variables describing the distribution and intensity of beetle boring and *H. thouarsianum* sporulation, and variables related to the site and the tree's position within the stand. The recursive partition model for all failure types is summarized in *fig. 5*. The presence of *H. thouarsianum* fruiting bodies provided the best first split of the data. Trees with *H. thouarsianum* were predominantly (82 percent) cases, whereas the group lacking *H. thouarsianum* were mostly (80 percent) controls. The second split for both halves of the partition tree was based on the presence of *Phellinus* fruiting bodies, most commonly *P. gilvus*. Cases were more likely than controls to have *Phellinus* fruiting whether or not they also had *H. thouarsianum* sporulation. Further splits were based on sky exposed canopy (higher percentage of cases where exposure was less than 50 percent), the presence of *I. andersonii* fruiting bodies (only present in failed trees), the distribution of *H. thouarsianum* stromata around the stem (cases more likely to have stromata around at least 50 percent of the stem circumference) and the presence of multiple branches arising from a single point, often as co-dominant stems (this defect was more common in cases).

We also constructed recursive partition models using bole and root crown failures as the outcome variable (not shown). This model used the same initial split (*H. thouarsianum* presence) as the model for all failures, and also included splits based on *Phellinus* presence and sky exposure. However, other variables included in this model differed from those in the model for all failures. Among trees with *H. thouarsianum* and lacking *Phellinus,* increased likelihood of failure was associated with one-sided (i.e., unbalanced) tree canopies, dead trees, and multi-stemmed trees.

Logistic regression models

Some of the explanatory variables that we evaluated are highly correlated with each other. In constructing logistic regression models, highly correlated explanatory variables can often be substituted for each other with relatively little change in overall model fit. Furthermore, highly correlated variables, when included in the same model, will often fail to be significant, even when they are known prognostic factors. The effects of the variables cannot be separated; only combined effects can be estimated. Variables related to the presence and abundance of beetle boring, *H. thouarsianum* sporulation, and the late or dead *P. ramorum* canker status were highly correlated. Variables describing these three factors usually cannot be included in the same model, but they can be substituted for each other in the model without greatly affecting model fit.

The best fitting models do not necessarily constitute the best models from the standpoint of predicting failure. Some variables are more readily detected or more precisely rated in failed trees than in intact trees, or vice versa. For instance, although both internal decay and ambrosia beetle boring are strongly associated with failures, they are much more evident on failed wood surfaces than in intact trees. While these factors can be fitted into multivariate models, they may not be as useful for predicting failure in intact trees. We avoided using variables in the reported models that were likely to be biased due to differences in ratings of the factors in intact and failed trees.

Figure 5— Summary of results of recursive partitioning model of all coast live oaks with failures (cases, n=106) and nonfailed controls (n=170).

Table 3 shows parameters for two models with nearly identical fit (based on AIC values) using combined data for all failure types. Model one includes the overall *P. ramorum* symptom status as a variable. Compared with asymptomatic trees or trees with only bleeding cankers (early *P. ramorum* symptoms), trees with more advanced disease symptoms were much more likely to fail. In model two, the presence of beetle boring and greater distribution of *H. thouarsianum* sporulation around the stem are both positively associated with failure. One or both of these agents were present in all trees with late *P. ramorum* symptoms. The other six variables that these two models have in common have nearly identical significance levels and odds ratios in the two models. Failure was more likely to occur in dead trees, trees that had *Phellinus* sporulation or canker rot symptoms, and trees in tree neighborhoods altered by adjacent or nearby failures or mortality. Failure potential also increased with the number of stems, but decreased with increasing levels of canopy exposure to the sky (i.e., increased dominance). No other predictors were consistently fitted into the best overall models for all failures.

Using the logistic regression models, a high probability of failure was predicted only if a number of factors are simultaneously present at levels that favor failure. This is consistent with field observations. We observed that even dead trees, which have an intuitively high failure potential, generally did not have large-diameter failures unless they exhibited other symptoms associated with decay and degradation (e.g., beetle boring, *H. thouarsianum* or *Phellinus* sporulation) or poor structural characteristics (e.g., multiple stems).

Overall failure patterns in trees with P. ramorum *canker symptoms*

Coast live oaks with severe *P. ramorum* canker symptoms typically followed one of several general patterns of failure characterized by different types of wood decay. These patterns were evident in both this study and in our related long-term disease progress study (Swiecki and Bernhardt 2004). The first failure pattern was common in trees with diameters up to about 30-40 cm. Many of these trees were healthy and sound prior to the onset of *P. ramorum* canker symptoms. These trees commonly experienced bole failures characterized by moderate to heavy colonization of the failed stem cross section by ambrosia beetles and extensive to nearly complete wood decay that originated in the outer sapwood and progressed inward. Fruiting of *H. thouarsianum* and/or *P. gilvus* was commonly present, suggesting that these were the among the primary sapwood decay fungi. Trees commonly failed after the top was completely dead, although some trees with green tops showed this failure pattern. Bole failure was commonly the first failure above the threshold size that occurred in these trees. This pattern of failure was not been observed in trees without *P. ramorum* canker symptoms, largely because no other mortality factors present in these areas kill otherwise vigorous trees in this size class.

A second failure pattern was seen in larger diameter trees that (1) had extensive *P. ramorum* canker symptoms, (2) were dead at the time of failure, and (3) were apparently healthy and largely unaffected by wood decay fungi prior to developing *P. ramorum* canker symptoms. Although the boles of these trees were also attacked by ambrosia beetles and *H. thouarsianum,* the depth of sapwood decay was insufficient to cause bole failure over the short term. As a result, these trees have remained standing for several to many years after death. The first above-threshold failures occurring in these trees were branch failures that resulted from wood decay and tunneling by wood-boring beetles. Boring by buprestid and cerambycid beetle larvae was commonly more prominent than ambrosia beetle boring in failed branches from these standing dead trees. After several years, progressively larger branches have failed as various wood decay fungi have degraded the wood. Some of these trees have eventually failed at the bole or root crown, especially if the tree canopy was unbalanced. Trees without *P. ramorum* canker symptoms in the study areas generally did not show this overall mortality/failure pattern.

A third failure pattern was seen in trees that had substantial amounts of pre-existing wood decay due to established infections by canker rot or other decay fungi. These failures often occurred in living stems and were characterized by extensive heartwood decay columns that were sometimes associated with cavities. In some trees, sapwood decay and beetle boring associated with *P. ramorum* canker symptoms had approached or merged with these heartwood decay columns, causing a critical loss in structural integrity that resulted in failure. Fruiting bodies of *I. andersonii* and, less frequently, *P. robustus* were sometimes associated with this type of decay and failure. However, fungal fruiting bodies were lacking on many failed trees with extensive heartwood decay. This failure pattern was involved in most of the large-diameter (greater than 50 cm diameter) bole, root crown, and branch failures, but also occurred in smaller diameter stems. Unlike the two previous patterns, failure due to extensive heartwood decay commonly occurred in trees without *P. ramorum* canker symptoms, although it appears that *P. ramorum* canker symptoms increased the likelihood of failure in trees which already had substantial amounts of heartwood decay.

Table 3— *Parameters and significance levels for multivariate logistic regression models for the case outcome (any failure over threshold size) in coast live oak (n=106 cases, 170 controls).*

	Model 1[1]		**Model 2**[1]	
Predictor variables	**P level**[2]	**Odds ratio (CI)**[3]	**P level**[2]	**Odds ratio (CI)**[3]
P. ramorum symptoms late or dead (vs. early or none)[c]	<0.0001	13.5 (5.28-39.1)	--	--
Beetle boring present	--	--	0.0030	5.99 (1.84-20.48)
Rating of percent stem circumference with *Hypoxylon* sporulation	--	--	0.0441	4.64 (1.04-23.2)
Number of stems from ground	0.0029	50.5 (3.64-787)	0.0038	42.5 (3.21-656)
Phellinus present	<0.0001	15.5 (5.17-56-2)	<0.0001	16.0 (5.21-59.5)
Canker rot present	<0.0001	5.35 (2.36-13.03)	0.0001	4.85 (2.12-11.8)
Tree dead	<0.0001	17.1 (5.39-65.8)	0.0001	13.5 (3.58-58.5)
Sky exposed canopy rating	<0.0001	0.0181 (0.00235-0.115)	<0.0001	0.018 (0.00232-0.117)
Altered neighborhood	0.0139	4.19 (1.32-14.9)	0.0032	5.80 (1.76-21.9)

[1] The Akaike Information Criterion (AIC) for models 1 and 2 were 171.3 and 174.3, respectively. Overall significance levels of for both models were p<0.0001.
[2] Likelihood ratio test significance level
[3] Odds ratios and 95 percent confidence intervals; odds ratios greater than 1 indicate that a factor is positively associated with the case (failure) outcome

Discussion

In the *P. ramorum*-affected coast live oak woodlands we studied, failure rates have increased markedly over the last five years (*fig. 1*). In particular, rates of bole failure and large branch failure were greatly increased in the 1.5 years prior to our survey (*fig. 1*). Most of the recent failures have occurred in trees with extensive *P. ramorum* canker symptoms that were already dead or had late disease symptoms, characterized by the presence of *H. thouarsianum* and/or wood-boring beetles. Failure risk in trees with *P. ramorum* canker symptoms was substantially increased only if the trees had been attacked by secondary wood degrading organisms.

Failure rates for the 1.5 year interval preceding the study survey were probably near the maximum that is likely to be observed in these stands in connection with the current disease outbreak. Observations from permanent plots have shown that few additional coast live oaks in these areas have developed *P. ramorum* symptoms between 2000 and 2004 (Swiecki and Bernhardt, these proceedings). Because more than 80 percent of the recent failures in this study occurred in trees with *P. ramorum* symptoms that were already dead and/or were colonized by secondary organisms (*fig. 2*), once most of these diseased trees have failed, the annual failure rate should decline substantially. Within our permanent plots, nearly 80 percent of trees with *P. ramorum* symptoms that were dead or had late symptoms in 2000 had failed by 2004, with the greatest number of failures occurring in 2002 and 2003 (Swiecki and Bernhardt 2004, unpublished). Hence, unless or until a large number of the remaining asymptomatic trees in these stands develop severe *P. ramorum* canker symptoms, the annual failure rate should decrease. If results in these plots are typical, we would expect that an outbreak of *P. ramorum* canker in a coast live oak stand is likely to be followed in several years later by a corresponding spike in the tree failure rate among killed and late-stage diseased trees.

Because *P. ramorum* can kill some trees relatively quickly, particularly trees that are otherwise some of the more vigorous trees in the stand (Swiecki and Bernhardt 2002a,b, 2004, these proceedings), we have found patterns of tree failure that are unique to trees with *P. ramorum* canker symptoms. These include main stem failures due to decay that originates in the sapwood and large branch failures occurring on large-diameter standing dead trees that were killed by *P. ramorum* canker. Hence, coast live oak stands affected by *P. ramorum* have both higher failure rates and different types of failures than are typical in stands that are free of *P. ramorum*.

Several lines of evidence implicate wood decay as the primary factor influencing failure potential in the stands we studied. Decay was present and rated as a contributing factor in almost all failures. Fruiting bodies of various wood decay organisms, decay columns, and canker rot symptoms were significantly more common among cases than controls. Also, variables related to decay were highly significant in both recursive partition and multivariate logistic regression models. The reduction in wood strength due to decay is a fundamental cause of almost all of the failures we observed. Similarly, in a study of oaks with stem failures conducted in the aftermath of Hurricane Hugo, 96 percent of failed (not windthrown) trees had internal decay (Smiley and Fraedrich 1992). Decay has also been implicated in failures among natural conifer stands (Coates 1997, Ruel 2000, Dunster 1996), but not among planted Monterey pine in a park setting (Edberg and others 1994).

We collected samples of decayed wood from many of the recently failed trees in this study to identify decay fungi present using DNA probes (M. Garbelotto, unpublished). Partial results compiled to date confirm that most decay samples were colonized by one to several wood decay fungi. In many of the samples, wood decay fungi identified by DNA detection methods were not observed fruiting on the affected stems. Further analyses of these samples will provide greater insight into the interactions of various decay fungi in coast live oaks affected by *P. ramorum*.

Fruiting bodies of *H. thouarsianum,* a sapwood-decaying fungus, were present on 82 percent all recent failures and 91 percent of the recent failures with *P. ramorum* canker symptoms. *H. thouarsianum* appears to be responsible for much of the sapwood decay seen in failures of trees with *P. ramorum* canker symptoms. Although the biology of *H. thouarsianum* has not been studied, most *Hypoxylon* species and similar fungi in the Xylariaceae colonize living hosts either as endophytes or through latent infections of woody tissue, and function as opportunistic pathogens of stressed trees (Ju and Rogers 1996). *Biscogniauxia atropunctata* and *B. mediterranea,* both of which were previously classified as species of *Hypoxylon*, initiate latent infections in healthy oaks and subsequently colonists decay the inner bark and sapwood when trees that have been stressed by drought (Sinclair and others 1987).

Wood degradation by wood boring beetles may also contribute to failure risk, but because beetle damage was so highly correlated with the presence of decay, we were not able to completely distinguish between the effects of decay and beetle boring. The lack of heavy beetle boring activity at the point of failure in many failed trees suggests that beetle boring is not the primary factor influencing failure potential. Nonetheless, the presence of extensive beetle activity is an indicator of increased failure potential in trees with *P. ramorum*, whether the effect is due to beetle tunneling itself or beetles are serving as an indicator of associated decay. This is especially the case in smaller–diameter trees that follow the first pattern of failure described above.

In a recent study on log sections from two failed coast live oak trees with *P. ramorum* cankers, sapwood decay appeared to proceed faster in logs that were heavily colonized by ambrosia beetles than in logs treated with permethrin to inhibit beetle colonization (Svihra and Kelly 2004). Logs used in that study were initially sound, about 40 cm in diameter or less, and were observed for 411 days. If beetle boring accelerates sapwood decay caused by *H. thouarsianum* and/or other fungi, beetles may play a role in determining how soon failure occurs in *P. ramorum*-infected trees that follow the first failure pattern described above. However, branch failures in large diameter trees (pattern 2 above) and failures in trees with existing heartwood decay (pattern 3) are less likely to be strongly influenced by amounts of beetle boring in the bole. It is far from certain that reducing scolytid beetle attack with insecticides will attenuate failure potential in trees that follow these two latter failure patterns.

Relatively few structural defects were strongly associated with tree failures in this study. Also, structure-related defects associated with failure in single-variable models (*table 2*) were not the same as those in multivariate models (*fig. 5, table 3*). Structural defects such as multiple stems or branches at one point, one-sided canopy distribution, and cavities either create a point of structural weakness or lead to uneven distribution of stress in the bole or branches. In coast live oak, it appears that sound wood is typically strong enough to prevent failure in the presence of these defects. Due to growth patterns in these forests, many live oak canopies are highly asymmetric and imbalanced, but failure rates are low among live, non-decayed trees. However, when wood strength is lost due to decay, these same defects may precipitate failure. Hence, in coast live oak, variables related to decay are generally much stronger predictors of failure potential than are structural defects related to canopy imbalance.

Two factors related to local stand structure were significant in various failure models. The first, sky-exposed canopy, measures the degree of overtopping or tree dominance within the canopy. In all models, lower levels of sky exposed canopy (i.e., greater amounts of overtopping) were associated with a higher risk of failure. Some of this effect is related to the presence of high levels of wood decay in severely suppressed understory trees, which generally did not exhibit *P. ramorum* canker symptoms. In addition, cooler, moister conditions in the understory may increase the activity of wood decay fungi in these trees.

The second variable related to stand structure in the models is the altered neighborhood variable. This factor indicates that failures in these stands tend to occur near other dead and/or failed trees. We have previously shown (Swiecki and Bernhardt 2001, 2002a,b) that *P. ramorum*-infected trees in these stands are clustered on a very local scale (i.e., within 8 m radius plots). Hence, spatial clustering of failures seen in this study is probably due in large part to the underlying spatial clustering of *P. ramorum* canker. However, many tree canopies also overlap and interlock in many of these stands, so loss of adjacent trees may result in loss of direct support and increased wind exposure, thereby increasing failure potential.

Results from the multivariate recursive partitioning and logistic regression models indicate that multiple factors contribute significantly to the chance that a given tree will fail. Given that several patterns of failure are found in these stands, it is logical that no single variable serves as a satisfactory predictor of failure. A high failure potential typically exists when multiple factors are at levels that favor failure. The logistic models also provide an idea of the relative magnitude of the effects of each factor. For example, late *P ramorum* canker symptoms (i.e., beetles and/or *H.*

thouarsianum present), tree death, and the presence of *Phellinus* sporulation have a bigger impact on failure potential than the presence of beetle boring, canker rot symptoms, or altered neighborhoods (*table 3*). Factors modeled as continuous variables are more difficult to rank because the range of observable values must be considered when interpreting the odds ratios. Among factors modeled as continuous variables, sky exposed canopy ratings have the greatest overall impact on calculated failure probabilities, followed by the number of stems and *H. thouarsianum* girdling.

The retrospective design used in our study allowed us to evaluate a large number of failures over a short time period and develop models that can be used to predict failure risk. We have used this data to develop guidelines for assessing failure potential in coast live oak stands affected by *P. ramorum* canker (Swiecki and Bernhardt 2003). Although we were able to evaluate many characteristics in failed trees, some factors were clearly assessed with less accuracy on fallen trees than standing ones, e.g., lean and some canopy distribution characteristics. In addition, most trees were evaluated many months after failure had occurred. Levels of some factors, such as the presence of fruiting bodies, may have been different at the time of observation than at the time of failure. If this is so, even if a factor (e.g., decay caused by *Phellinus*) is related to failure, the rated variable (e.g., *Phellinus* sporulation) may be less useful as a predictor than is implied by the models.

These limitations can be overcome by conducting a prospective evaluation of trees that may fail. Because annual failure rates are typically low, to observe sufficient numbers of failures and the factors associated with them, prospective studies generally require very large sample sizes and observations over an extended time period. In our related study (Swiecki and Bernhardt 2001, 2002a,b, 2004, these proceedings), we are prospectively evaluating tree failure in *P. ramorum*-affected stands. This prospective data will be used to refine models developed in our retrospective study.

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