Patterns of Mortality in an Old-Growth Mixed-Conifer Forest of the Southern Sierra Nevada, California

Thomas F. Smith, David M. Rizzo, and Malcolm North

ABSTRACT. Mortality patterns in an old-growth, mixed-conifer forest, in the absence of wildfire, were investigated at the Teakettle Experimental Forest from 2000 to 2002. We tested the hypothesis that after a century of fire suppression, pathogen- and insect-associated mortality (between episodic droughts) would be significantly greater on ingrowth trees (i.e., smaller-diameter, shade-tolerant species in high-density clusters). Using a survey of over 30,000 mapped trees, overall mortality, as measured by standing dead trees, was 8.7% of all stems ≥5 cm dbh. Mortality levels were proportional to the population size of the five dominant conifer species, white fir (*Abies concolor*), red fir (*A. magnifica*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana).* There was also no significant difference in mortality between shade-tolerant and shade-intolerant species. All dead trees were clustered within plots. Mortality was significantly higher than expected for large-diameter trees (>100 cm dbh) with all conifer species combined and for each individual species, except Jeffrey pine. Small-diameter dead trees were grouped in high-density clusters. Mortality was less than expected among small-diameter trees (5–20 cm dbh) for all species combined, red and white fir, and sugar pine. Mortality for all conifers was higher than expected in areas of high stand density and lower in areas of low stand density. Mortality of small-diameter trees was clustered and particularly high in areas of high stand density. Our data suggest pathogen- and insect-associated mortality is significantly greater in areas of high stand density but it is not higher for shade-tolerant species. Furthermore, mortality is higher than expected for large-diameter trees, suggesting an acceleration of old-tree mortality under current fire suppression conditions. FOR. SCI. 51(3):266–275.

Key Words: Canopy gaps, density-dependent mortality, dwarf mistletoe, bark beetles, root rot.

FOREST HEALTH IN WESTERN FORESTS has become a significant concern as large-scale mortality has increased in the last several decades (Wickman 1992, Campbell and Liegel 1996). Although there are many definitions of forest health (see Kolb et al. 1994), most mention that unhealthy forests have mortality levels outside the historic range of variability. A number of studies have suggested that increases in stem density and reduction of tree species diversity with fire suppression increase the scale and severity of tree mortality (Kilgore 1973, Wickman 1992, Savage 1997, Ferrell 1996, Campbell and Liegel 1996, Ansley and Battles 1998). In the absence of fire, insects and pathogens are the principal cause of mortality in Sierran forests, yet we have little information on how this mortality affects stand structure, composition, and spatial patterns of trees.

Most Sierran research has examined changes in density and species composition from fire suppression (Riegel et al. 1988, Parsons and DeBenedetti 1979) and how these changes have affected overall rates of mortality over time (Barbour et al. 2002, Mutch and Parsons 1998). Other research has detailed mortality resulting from severe droughts or insect epidemics (Macomber and Woodcock 1994, Campbell and Leigel 1996) in old-growth and second-growth mixed-conifer stands. There has been less research on chronic levels of pest mortality that occurs between episodic outbreaks in fire-suppressed forests. Ferrell (1996) suggested that insects and pathogens, by concentrating on high-density, stressed trees, might act as a corrective mortality agent, shifting stem density and species composition toward more historic conditions. It is not clear what current patterns of pest mortality in fire-suppressed old-growth are, and how stand structure and composition are being affected. As forest management has begun to emphasize restoring old-growth habitat to precolonization conditions (SNEP 1996), it is necessary to understand the patterns of mortality and what roles insects and pathogens have on stand structure and change.

We investigated spatial patterns of mortality in an old-growth, mixed-conifer forest in the southern Sierra Nevada of California. Throughout the Sierra, a century of fire suppression has increased stem density and shifted species composition toward shade-tolerant white fir and incense cedar. We conducted our research in old-growth to focus on

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pest mortality patterns in fire-suppressed forest conditions without confounding this effect with thinning and burning treatments common in managed stands. Our objective was to examine pest mortality effects on species composition, diameter size class distribution, and local stem density within a mixed-conifer forest. Specifically, we examined three questions concerning of stand structure affected by mortality. First, is pest-induced mortality proportional or higher than expected for shade-tolerant species? Second, is mortality proportional or higher than expected on small diameter trees in the stand? Finally, do trees in areas of high stand density have greater than expected mortality? We examined these potential aspects of mortality at three scales: the individual tree, the plot (4 ha), and the Teakettle landscape (72 ha).

Methods

Study Area

Research was conducted at the Teakettle Experimental Forest (TEF) in the King's River Ranger District of Sierra National Forest, approximately 80 km east of Fresno, CA. The forest (36º58′N, 119º2′W) is approximately 1,300 ha in size and ranges in elevation from 1,880 to 2,485 m. Soils are predominantly poorly developed and granite-based Inceptisols and Entisols with a coarse sandy loam texture and very low clay content. The climate is typical of the southern Sierra Nevada with hot, dry summers and cool, moist winters. Precipitation averages 1,250 mm per year and falls mostly as snow between the months of Nov. and Apr. Air temperatures range from a summer mean of 17.1°C to a winter mean of 1.2°C (North et al. 2002).

Mixed-conifer stands cover approximately 85% of the total area of TEF. The dominant tree species are white fir (*Abies concolor*), red fir (*A. magnifica*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*). Hardwood species are primarily found in the understory and account for less than 1% of the total basal area of the forest. White and red fir combined total about 85% of the total basal area found at TEF (North et al. 2002).

Historically, fires occurred approximately every 17 years within the TEF (North et al. 2002). There has not been a widespread fire at TEF since 1865 (North et al. 2005). TEF is an old-growth forest that has never experienced significant logging. Before recent experimental thinning research conducted after this study, only hazard trees had been removed along with some sugar pines as part of early white pine blister rust control efforts (North et al. 2002).

Study Species

White fir is the dominant species in the TEF. It is shade-tolerant and had rapid growth when young (Burns and Honkala 1990). The most damaging agents of white fir are fire, the fir engraver beetle (*Scolytus ventralis*), annosus root rot (*Heterobasidion annosum*), and dwarf mistletoe (*Arceuthobium abietinum* f. sp. *concoloris*). Red fir is also shade-tolerant when young (Burns and Honkala 1990), but is less common at TEF and more irregular in its distribution through the mixed-conifer stands. The species is also susceptible to the fir engraver beetle, annosum root rot, and dwarf mistletoe (*Arceuthobium abietinum* f. sp. *magnificae*) (North et al. 2002).

Incense cedar is considered to be less shade-tolerant than the two fir species but more shade-tolerant than associated pine species. Young incense cedar trees are very susceptible to fire damage and related mortality (Burns and Honkala 1990). The main pathogens of the species at TEF are true mistletoe (*Phoradendron juniperinum* subsp. *libocedri*), broom rust (*Gymnosporangium libocedri*), and trunk rot (*Oligoporus amarus*) (North et al. 2002).

Teakettle's two pine species, Jeffrey pine and sugar pine, are considered to be shade-intolerant (Burns and Honkala 1990). The main mortality agents for Jeffrey pine are Elytroderma needle disease (*Elytroderma deformans*), dwarf mistletoe (*Arceuthobium campylopodium*), and the Jeffrey pine beetle (*Dendroctonus jeffreyi*). The major diseases and insects of sugar pine are the introduced white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and dwarf mistletoe (*Arceuthobium californicum*) (North et al. 2002).

Field Sampling

Eighteen permanent 4-ha plots had previously been established as part of long-term ecosystem research at Teakettle (North et al. 2002). Plots are 200 × 200 m squares and replicated by tree structure and species composition using variogram and cluster analysis (North et al. 2002). Plots were sized to include the range of structure and compositional variability found in mixed-conifer and then located to replicate stem density, basal area, and species composition. Each plot includes a nearly equal mix of the three dominant patch types found in the forest: closed canopy (>75% canopy cover), open canopy (<25% canopy cover), and mountain whitethorn (*Ceanothus cordulatus*) shrub patches (North et al. 2002). Within each of the 18 plots, every tree and snag larger than 5 cm dbh was identified, measured, mapped, and tagged.

Information was recorded for all trees within the study plots before experimental thinning or prescribed burning activities during the summers of 2000–2002. Data were collected for each individual, including the tree's position in the canopy as dominant, co-dominant, intermediate, or suppressed. Standing dead trees were identified to species and the cause or causes of death determined whenever possible. Recent deaths were determined by the retention of foliage and bark and the condition of the wood of the tree (Tallent-Halsell 2004). Logs were generally not investigated because of the difficulty of determining species, size, and cause of death when in advanced stages of decay. The crown, trunk, and base of each tree were examined for signs and symptoms of diseases and insects (Hansen and Lewis 1997, Furniss and Carolin 2002, Geils et al. 2002, Sinclair et al. 1987, Wood et al. 2003). The majority of insects and diseases found at TEF are specific to just one or two hosts (North et al. 2002). Trunks were examined for typical boring dust and pitch tubes of bark beetles, and bark was removed from snags to search for distinctive beetle galleries. Fungal fruiting bodies from trunks or growing from root systems were identified. After trees were cut following a later experimental thinning study, the stumps were examined for the presence of characteristic root rot decay patterns (Otrosina and Scharpf 1989, Woodward et al. 1998). Stem pathogens (dwarf mistletoes and rust diseases) were identified from stems and branches. Dwarf mistletoe infection was rated according to standard procedures (Hawksworth 1977). Any additional distinctive aspects of the trees' condition were also recorded including fire scars, wounds, dead tops, and general health conditions.

Statistical Analysis

Expected versus observed levels of mortality were compared using chi-square analyses and a significance level of $P < 0.05$ (O'Mahoney 1986). Expected mortality was presumed to be proportional to the overall species composition or size class frequencies for the entire study area (total sample of more than 30,000 trees). Analyses were conducted at the plot scale and the landscape scale by combining data from all plots (a total of 72 ha) to approximate the overall landscape. All *P*-values for significance were determined at the $<0.05\%$ confidence level.

Spatial relationships were analyzed for each plot separately using Ripley's K spatial point pattern analysis (SPPA Version 2.0 ©2003–2005, Peter Haase) to determine whether or not selected trees were clustered, random, or regular in distribution. Ripley's K compares distances between all location points in the same plane (Ripley 1979, Diggle 1983) using the reduced second moment measure or K function to examine spatial associations over a greater range of scales than nearest-neighbor analysis. In each plot, to evaluate significant departures from a random distribution, we calculated 95% confidence intervals using 100 Monte Carlo simulations (Andersen 1992, Haase 1995).

Most measures of tree density have focused on total density at the stand level. To examine the effects of density on mortality at the individual tree level, stem maps were used and a density index for each tree calculated in ARC/INFO using Theissen (i.e., Voroni) polygons (Mithen et al. 1984, Kenkel et al. 1989). The size and distribution of Theissen polygons has been commonly used to evaluate the impact of density, growing space, and competition of neighboring plants on plant succession (Mithen et al. 1984, Kenkel et al. 1989). The area around each tree is bisected by an equidistant line between adjacent stem locations, and the lines are connected to form a polygon around each tree location. The polygon's area is a rough approximation of the potential growing space, in square meters, for an individual tree. Polygon size is a function of local stand density, with smaller areas indicative of dense, "dog hair" conditions. Polygons were further weighted by dividing each polygon's area by the basal area of the individual tree to take into account the greater growing space demands (i.e., light, water, and nutrients) of larger trees. The resulting density values were used to compare mortality levels for trees at varying density levels.

In this study we focused on assessing density at the individual tree level. The smaller the density value, the more dense the stand around a particular tree, indicating a localized clustering of trees. Examining the distribution of density scales for all trees at TEF, we found four general ranges in density which we used in our analyses: class I (very high density, range 0–100, average of approximately 2,500 trees/ha); class II (medium/high density, range 100–500, approximately 1,000 tress/ha); class III (medium/low density, range 500–2,000, approximately 500 trees/ha); and class IV (very low density, range >2,000 average of approximately 250 trees/ha).

Results

General Mortality

A total of 31,868 trees were examined across the 18 plots. Tree mortality was measured as the cumulative number of standing dead trees found in the plots. Cumulative mortality on individual plots ranged from 5.3% to 13.1% of the total standing trees, with a mean of 8.7% (Table 1). Almost all dead trees appeared to have died more than 1 year previously. All but approximately a dozen trees per plot showed signs of earlier mortality such as loss of foliage, loss of bark, or advanced wood decay. Very few trees among all the species had signs, such as dead needle retention, of having died within the year previous to data collection.

Mortality by Shade Tolerance

Percentage mortality varied by species among the individual plots, but across the landscape mortality as a percentage of total trees was not significantly different for the different conifer species (Table 1). White fir was the dominant species among both the living and the dead trees in all of the plots. Dead trees constituted 9.2% of all the standing white firs, with a range of 3.5 to 17.7% among the various plots (Table 1). Similar levels of mortality were found for red fir (8.7%), incense cedars (5.1%), Jeffrey pine (8.5%), and sugar pine (8.6%) despite these species having far fewer numbers of individuals than white fir (Table 1). Levels of mortality of the shade-tolerant species and shade-intolerant species were not significantly different according to chi-square analysis (Figure 1).

Spatial Distribution of Mortality

Ripley's K analysis across all 18 plots consistently indicated a high clustering of all stems, all white fir, and all dead trees. It is difficult to quantitatively compare different analysis done in Ripley's K because results are particular to the stem distribution used in each analysis. In each of the 18 plots the degree of clustering was higher for dead white firs (Figure 2A) than for all white fir stems (Figure 2B) as

Table 1. Total numbers of trees and snags ≥ 5 cm dbh at the Teakettle Experimental Forest

	Number for all 18 Plots[a]	Average per Plot[a]	Average per Hectare	Range
Total Number of trees	31,868	1,770.4	442.6	1,121–2,434
White fir	20,953	1,164.1	291.0	809–1,590
Red fir	970	53.9	13.5	0–502
Incense cedar	5,281	293.4	73.4	6–617
Jeffrey pine	1,536	85.3	21.3	9–198
Sugar pine	2,440	135.6	33.9	24–262
Other[b]	760	42.2	10.6	0–275
Overall mortality				
Total Number of dead trees	2,757	152.2	38.1	86–318
% of total trees dead	8.7	8.6	8.6	5.3–13.1
% of dead white fir[c]	70.6	68.5	68.5	51.4–90.2
% of dead red fir[c]	3.0	4.0	4.0	0.0–33.0
% of dead incense cedar[c]	9.6	9.7	9.7	0.0–24.8
% of dead Jeffrey pine[c]	4.6	5.4	5.4	0.0–14.1
% of dead sugar pine[c]	7.8	8.2	8.2	0.5–23.2
% of dead other[b,c]	4.8	4.3	4.3	0.0–8.2
Percent of each species dead				
White fir	9.2	9.2	9.2	3.5–17.7
Red fir	8.9	6.2	6.2	0.0–75.0
Incense cedar	5.1	4.1	4.1	0.0–9.0
Jeffrey pine	8.5	10.4	10.4	0.0–26.3
Sugar pine	8.6	9.6	9.6	2.9–25.0
Other[b]	18.4	13.5	13.5	0.0–43.5

[a] Each plot was a square 4 ha in size (combined area of 72 ha).

[b] Other includes hardwoods and snags that could not be identified to species.

[c] Listed as percentage of total number of dead trees.

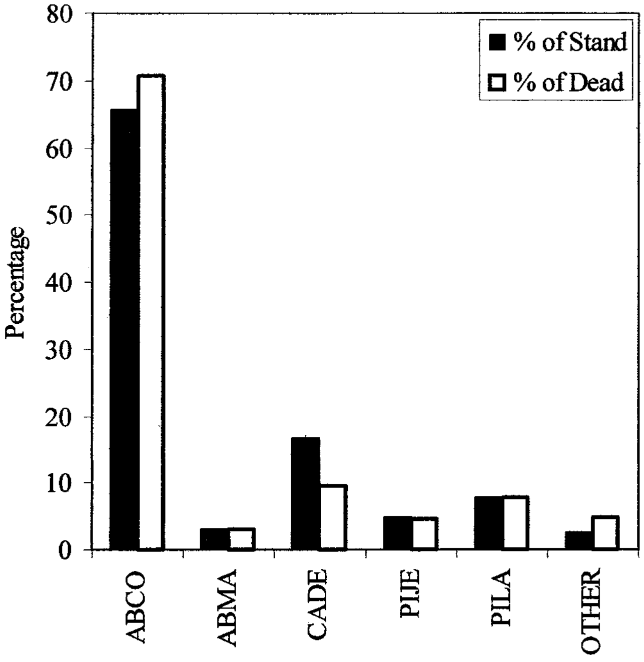

Figure 1. A comparison of dead and live trees, but percentage at the Teakettle Experimental Forest. Percentage of stand is the percentage of all trees in the plots that are of that species. Percentage of dead is the percentage of dead trees that are of that species. ABCO, *Abies concolor*; ABMA, *Abies magnifica*; CADE, *Calocedrus decurrens*; PIJE, *Pinus jeffreyi*; PILA, *Pinus lambertiana*; OTHER, various hardwoods and unidentifiable conifer snags.

indicated by the greater relative distance between the actual distribution and the 95% confidence interval attained when analyzing dead stems. Significant clustering of dead white fir and all white fir occurred at a scale of 0–60 m. Not enough dead individuals of other conifer species existed in each plot to conduct statistically valid analyses with Ripley's K analysis.

Mortality by Tree Diameter

Across the landscape, mortality varied by diameter classes for all of the conifer species (Figure 3). White fir, red fir, and sugar pine, as well as all tree species combined, had significantly less mortality in the 5.0–20.0 cm dbh class than expected if mortality were proportionally distributed across size classes. Jeffrey pine had significantly more mortality in the 20.1–40.0 cm dbh class than expected. Incense cedar recorded higher mortality in the 5.0–20.0 cm dbh class and lower in the 20.1–40.0 and 40.1–60.0 cm classes. The majority of mortality in Teakettle Forest was in the smallest diameter (5.0–20.0 cm dbh) class for all conifers (35.9%) and for the two main shade-tolerant species (31.6% of all dead white fir and 69.6% of all dead incense cedars) (Figure 3). Dead small-diameter trees (5.0–20.0 cm dbh) were typically more highly clustered (Figure 2C) at the plot scale when compared to all small-diameter trees combined (Figure 2D).

Throughout the stand, higher levels of mortality occurred in the largest diameter class (>100.1 cm dbh) for the stand as a whole and for the shade-tolerant white fir, red fir, and incense cedar and shade-intolerant sugar pine. Red fir also experienced significantly higher than expected mortality in

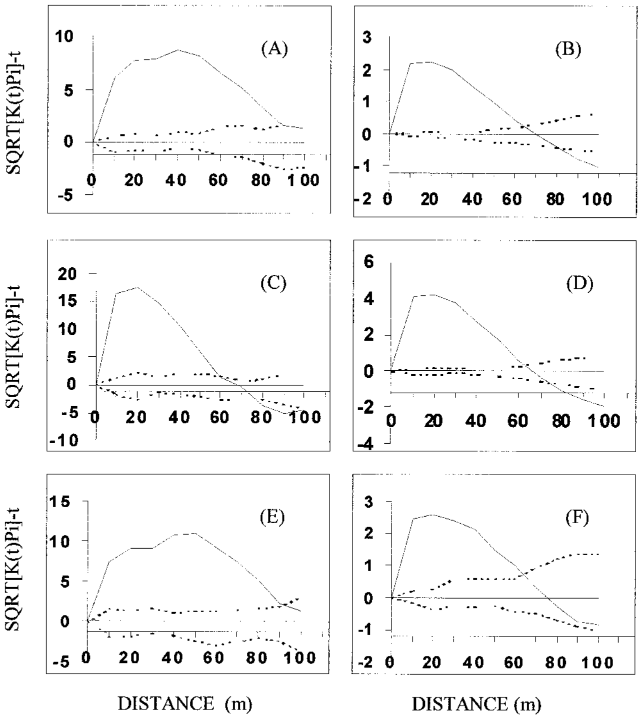

Figure 2. A comparison of the spatial distribution of dead trees by species, size class, and density with all trees for the same categories. Examples shown were taken randomly from plot BC1, which was typical of the spatial pattern found in the other 17 plots. The *y* axis shows the relative extent of clustering (the higher the number the greater the clustering) and the *x* axis shows the distance of clustering. (A) dead white firs, (B) all white fir stems, (C) dead trees 5–20 cm dbh, (D) all small stems 5–20 cm dbh, (E) dead trees in dense areas (average stand density of 2,500 trees/ha), (F) all trees in dense stand areas (average density of 2,500 trees/ha). Ripley's K analysis indicates significant clustering when the solid line (actual stem distribution) rises above the dotted lines (95% confidence intervals).

the next two largest diameter classes (60.1–80.0 and 80.1–100.0 cm dbh). Jeffrey pine was the one species that did not exhibit higher than expected mortality for large-diameter trees (Figure 3).

Mortality by Stand Density

Stand density had a major impact on mortality as measured by standing dead trees. The areas of greatest density (class I, weighted density scale 0–100, average of approximately 2,500 trees/ha) included 26.2% of all trees, but had the most mortality (42.3%) (Figure 4). Within these dense areas of the stand, mortality was also clustered as indicated by Ripley's K analysis (Figure 2E). At the plot scale, all trees found in the densest areas (class I) were clustered (Figure 2F). However, a qualitatively greater level of clustering was found for dead trees in the same dense areas of each plot according to Ripley's K analysis (Figure 2E).

Among the diameter classes, density had the greatest impact on mortality of small-diameter trees (5–20 cm dbh). In the densest parts of the stand (class I) mortality (5.2%) is higher than expected (2.5%). It is significantly higher among the small-diameter trees in the 100–500 density range (class II, average density of 1,000 trees/ha). Mortality is significantly lower for small-diameter trees in the least dense areas of TEF (4.1% versus an expected 40.1% for the class III, average of 500 trees/ha density, and 17.4% versus an expected 36.0% for the class IV, average density of 250 trees/ha) (Figure 5).

Causes of Mortality

A total of 57.7% of standing dead trees exhibited indications of one or more major insect or disease problem that may have contributed to the death of the tree. Among the dominant white firs both living and dead, 34.8% showed signs of attack by the fir engraver beetle or other wood-boring insects. White fir dwarf mistletoe was found in 24.8% of the white fir whereas only 1.2% of white fir showed obvious signs or symptoms of annosum root rot. However, the incidence of insects and pathogens varied considerably among the plots at TEF. It was also difficult to determine the exact pathway of mortality for most dead trees because of the length of time since death of the tree and the occurrence of numerous opportunistic insects and pathogens.

Discussion

Overall tree mortality at TEF is comparable to other old-growth Sierran mixed-conifer forests. Cumulative mortality as measured by standing dead trees in the Teakettle plots was only 8.7% as compared to cumulative mortality of 14.0% (range 3–33% across a series of plots) in mixed-conifer old-growth forests of the Lake Tahoe Basin (Barbour et al. 2002). In the Sierra San Pedro Martir National Park of Baja, Mexico, where fire suppression has not occurred, cumulative mortality in mixed-conifer old-growth was found to be 12.7% (range 4–15% across a series of plots) (Maloney and Rizzo 2002b). The TEF falls within both of these ranges.

Although mortality varied across the forest and by species, the total amount was not extremely high. The mortality rate is not known because data were collected for each plot in only a single year. However, the observed tree mortality had been spread over numerous years as indicated by the advanced wood decay and numerous secondary pests and diseases found on most dead trees. Few trees, around one dozen per plot, showed indications of recent death such as retention of dead foliage. Likely rates of mortality would compare favorably to rates of 0.5 to 1.5% (average 0.6 and 0.8%/year in the two stands) found by other researchers in mixed-conifer forests in prefire conditions (Mutch and Parsons 1998).

The TEF is typical of most Sierran mixed-conifer forests (SNEP 1996) in that, following a century of fire suppression, white fir and incense cedar regeneration has increased stand density and shifted species composition toward more shade tolerants (Barbour et al. 2002, Minnich et al. 1995). In the absence of fire, the effects of pathogens and insects on stand structure and composition are largely unknown. Ferrell (1996) suggested pest mortality might be higher on regeneration since fire suppression because these stems

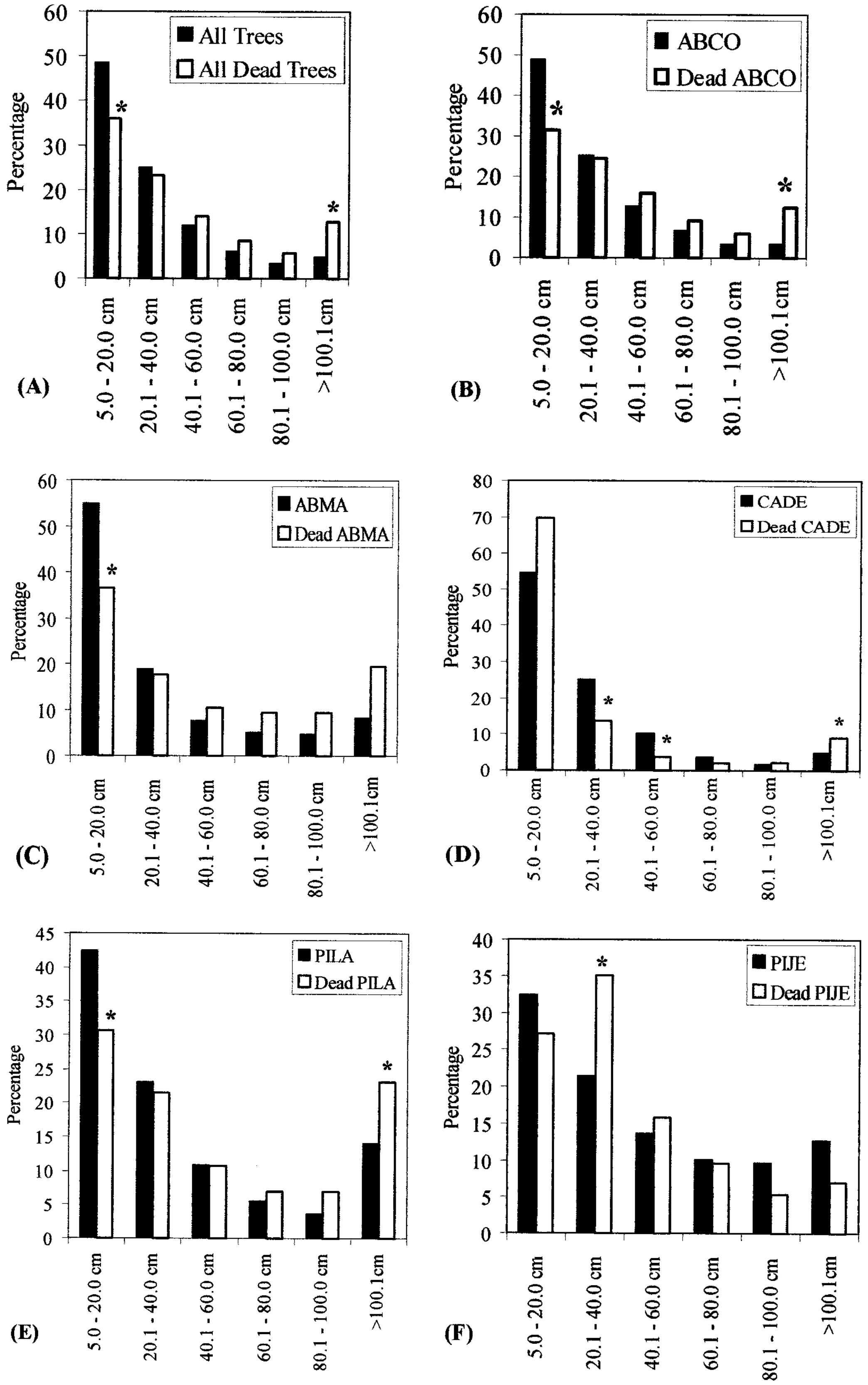

Figure 3. Variability in mortality by diameter class. Left-hand bars show the percentage of all standing trees in that class. Right-hand bars are the percentage of all standing dead trees in that class, * indicates that the percentage of mortality is significantly different from the overall percentage for that class (chi-squared analysis, $P < 0.05$). Charts are for (A) all trees combined, (B) white fir (*Abies concolor*), (C) red fir (*Abies magnifica*), (D) incense cedar (*Calocedrus decurrens*), (E) Jeffrey pine (*Pinus jeffreyi*), and (F) sugar pine (*Pinus lambertiana*).

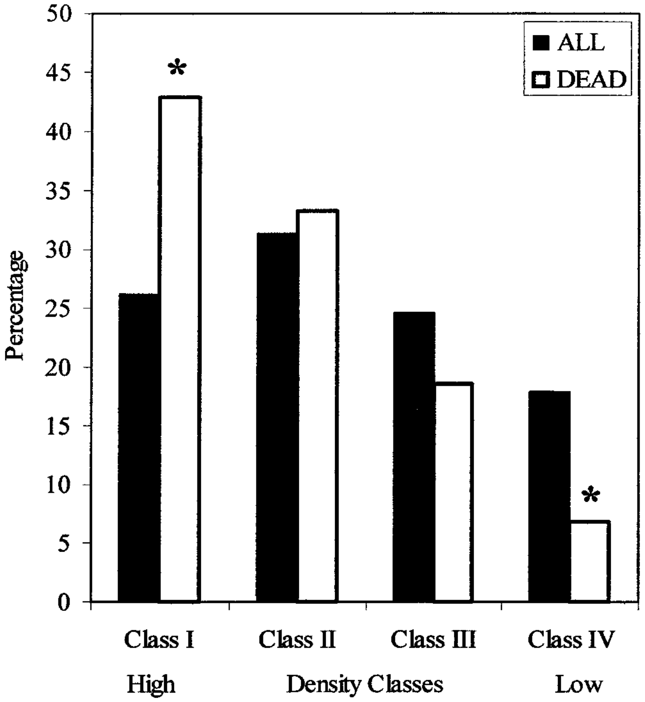

Figure 4. Percentage of mortality by density class. Left-hand bars are the percentage in that class of the total number of trees. Right-hand bars are the percentage of total standing dead trees in that class. Density classes are class I (very high density, range 0–100, average density of 2,500 trees/ha), class II (medium/high density, range 100–500, average density of 1,000 trees/ha), class III (medium/low density, range 500–2,000, average density of 500 trees/ha), and class IV (very low density, range >2,000, average density of 250 trees/ha). *, The percentage for dead trees is significantly different from the percentage of total trees in that category.

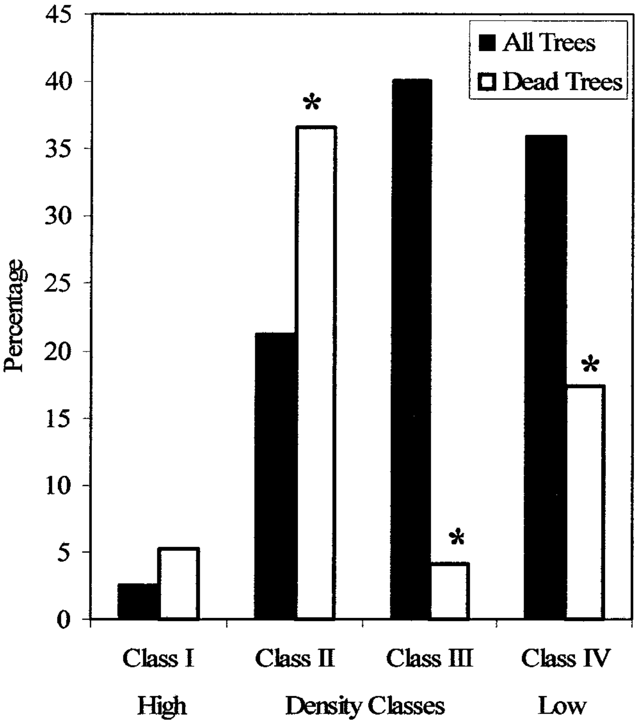

Figure 5. Percentage of mortality for small diameter trees (0–20 cm dbh) by density class. Left-hand bars are the percentages in that class of the total number of small diameter trees. Right-hand bars are the percentage of dead small diameter trees in that class. Density classes are class I (very high density, range 0–100, average density of 2,500 trees/ha), class II (medium/high density, range 100–500, average density of 1,000 trees/ha), class III (medium/low density, range 500–2,000, average density of 500 trees/ha), and class IV (very low density, range >2,000, average density of 250 trees/ha). *, The percentage for dead trees is significantly different from the percentage of total trees in that category. Few small-diameter trees appear in the densest areas due to the weighting of density by dividing by the basal area of the individual tree.

would be highly clustered, creating greater drought stress and easier transmission of pathogens. In this study, we examined this idea of pests as a corrective mortality agent in fire-suppressed stands by focusing on three corollaries (implications) of this hypothesis; insect- and pathogen-associated mortality would be higher on trees in high-density clusters, on shade-tolerant species, and on small-diameter trees.

Density-dependent mortality does appear to be a driving force of stand-structure change at TEF. Dead trees were more likely to be found in areas of greater stand density. Both analyses, Ripley's K and chi-square by density class, found significant clustering of standing dead white firs, small-diameter dead trees, and dead trees in dense stand areas. All trees, however, both living and dead, appear to be clustered in the TEF. The patchy nature of old-growth mixed-conifer forests creates a certain amount of clustering (North et al. 2004). Although difficult to compare in quantitative fashion with Ripley's K analysis, mortality clustering appears to be greater than the clustering for all trees. The chi-square analysis supports this inference, indicating higher than expected mortality in the high-density classes. Small trees in particular suffered significantly more mortality in dense areas than in open parts of the stand.

Other researchers have found varying relations among stand density, stand structure, and mortality. North et al. (2004) noted that the Wind River old-growth forest in the Pacific Northwest had an overall regular stem distribution compared to the patchy nature of TEF. Song et al. (2004) found distinct canopy clustering and species variability in an old-growth Douglas-fir forest. Chen and Bradshaw (1999) believed that the nonrandom formation of canopy openings from tree mortality was the primary reason for species aggregation in an old-growth spruce-fir forest in China.

Tree mortality still occurred in areas of low stand density at TEF. The spatial distribution of trees across the stand is irregular, with many canopy gaps and areas of extremely low stand density (North et al. 2002). Such areas may contain shallow soil depth to bedrock that would potentially place trees under moisture stress and lead to death. Open areas also have higher temperatures during summer months than dense stand areas, creating more potential moisture stress.

Density may be correlated with high tree mortality for several reasons. High stand density allows for easier transmission of root diseases via root-to-root contact (Woodward et al. 1998), although few infected small trees will show indications of attack (Otrosina and Scharpf 1989). In the

Wind River old-growth forest of the Pacific Northwest, root diseases were minor causes of tree death, but suspected of leading to most wind-throw mortality (23% of all mortality) (Shaw et al. 2004). The spread of dwarf mistletoe seeds is more likely in dense stands (Reich et al. 1991), especially in areas of low species diversity and few intervening nonhost species (Maloney and Rizzo 2002a). Bark beetles such as the fir engraver beetle tend to be more severe in attacks in areas of high density (Ferrell and Smith 1976, Paine et al. 1997) and increase in activity when trees are stressed due to competition and suppression (Ferrell et al. 1994). Sierran mixed-conifer forests receive little rain between May and Oct. and drought is a common stressor, particularly in low snowfall years. In areas of high stand density, moisture stress may be particularly acute.

Tree mortality is rarely caused by a single agent; pest complexes (e.g., root diseases/bark beetles, dwarf mistletoe/bark beetles, or root diseases/dwarf mistletoe/bark beetles), sometimes in conjunction with abiotic stress factors (e.g., drought), are often responsible for tree death. In addition, opportunistic or secondary insects and pathogens often obscure the primary agents of mortality. Indications of known tree-killing insects and pathogens did exist on the majority of standing dead trees. Much of TEF's mortality may have occurred during the last drought between 1987 and 1992. In a wildlife snag survey conducted at Teakettle between 1988 and 1997, the number of dead trees over 21 ha increased significantly between 1988 and 1991, but then fell and remained constant from 1993 to 1997 (North et al. 2002).

There was not a strong correlation between tree mortality and shade tolerance in the TEF. Shade-tolerant species such as white fir and incense cedar did comprise the majority of dead trees, but at rates comparable to their relative proportions in the stand. In fact, mortality rates were remarkably consistent across species, with mortality generally proportional to the percentage of each species in the composition of live trees.

Tree size was correlated with mortality but contrary to what was expected. Although the majority of dead trees are in the small-diameter classes, the percentage is significantly less than the percentage of small-diameter live trees. Only Jeffrey pine has a higher than expected percentage of mortality in a small-diameter class (20.1–40.0 cm dbh). All other species have significantly less than expected mortality in the 5.0–20.0 cm dbh class. Furthermore, in the large-diameter class, mortality is significantly greater than expected for all species except Jeffrey pine. At TEF, Jeffrey pine often grows in low-density conditions on shallow ridgetop soils, where fire suppression has caused few changes in stand structure (North et al. 2005).

There appear to be two types of mortality factors at work in the TEF. Density-dependent mortality particularly affects smaller-diameter trees through competition for resources and self-pruning. Density-independent mortality appears to be more important for larger-diameter trees and is primarily pest-induced. Larger-diameter trees tend to be found in more open areas of the stand and exhibit greater levels of diseases and insects than smaller-diameter trees. Larger trees have had more time for chronic attacks by pests to occur. However, smaller-diameter trees do not always exhibit dramatic symptoms of attack by pests even when they are present. Small-diameter trees tended to exist in denser stand areas where spread of diseases and insects is more likely, but stress due to competition and shading may be more important than pests.

Higher than expected detection of mortality in the large-diameter classes, however, is at least partially due to a bias from slow decay rates associated with large trees. Dead large trees represent a longer recording period than the relatively ephemeral period over which small trees die, decay, and disappear. We do not know of a way survey data can correct for this bias and therefore this result should be viewed with caution. More long-term research is needed to examine rates of large tree mortality. It is, however, an unexpected result that warrants concern because logging has already reduced the number of large, old trees in the Sierra and all of the current restoration plans call for maintaining and increasing the number of old-growth trees.

Our data suggest that an increase in stems due to fire suppression or climate change has overwhelmed the corrective nature of mortality by native pathogens and insects. Pest mortality is not higher on either shade-tolerant species or small-diameter sizes, but is significantly greater than expected on large, old-growth trees. Mortality is also high in high-density potions of the forest, and this clustered mortality helps to create gaps needed to allow shade-intolerant pines to regenerate. Although longer-term observations are necessary, mortality initiated by insects and diseases and other causes may help to perpetuate species diversity (Goheen and Hansen 1993, Haack and Byler 1993, Van der Putten 2000) and maintain the mixed-conifer composition of TEF's old-growth forest. A greater understanding of the patterns and processes of tree mortality will be important in the restoration and maintenance of old-growth forest conditions.

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