Mixed Conifer Forest Mortality and Establishment Before and After Prescribed Fire in Sequoia National Park, California

Linda S. Mutch and David J. Parsons

ABSTRACT. Pre- and post-burn tree mortality rates, size structure, basal area, and ingrowth were determined for four 1.0 ha mixed conifer forest stands in the Log Creek and Tharp's Creek watersheds of Sequoia National Park. Mean annual mortality between 1986 and 1990 was 0.8% for both watersheds. In the fall of 1990, the Tharp's Creek watershed was treated with a prescribed burn. Between 1991 and 1995, mean annual mortality was 1.4% in the unburned Log Creek watershed and 17.2% in the burned Tharp's Creek watershed. A drought from 1987 to 1992 likely contributed to the mortality increase in the Log Creek watershed. The high mortality in the Tharp's Creek watershed was primarily related to crown scorch from the 1990 fire and was modeled with logistic regression for white fir (*Abies concolor* [Gord. and Glend.]) and sugar pine (*Pinus lambertiana* [Dougl.]). From 1989 to 1994, basal area declined an average of 5% per year in the burned Tharp's Creek watershed, compared to average annual increases of less than 1% per year in the unburned Log Creek watershed and in the Tharp's watershed prior to burning. Post-burn size structure was dramatically changed in the Tharp's Creek stands: 75% of trees ≤50 cm and 25% of trees >50 cm were killed by the fire. For. Sci. 44(2):341–355.

Additional Key Words: Percent crown volume scorched, fire severity, binary logistic regression, demography.

Little published information exists on tree mortality and establishment patterns in the forests of the southern Sierra Nevada of California. Numerous studies have explored presettlement fire history in Sierra Nevada mixed conifer forests (Kilgore and Taylor 1979, Swetnam et al. 1992, Swetnam 1993). Bonnicksen and Stone (1982) reconstruct pre-Euro-American forest conditions in a giant sequoia-mixed conifer forest and compare these to present conditions. They also examine the effects of a prescribed fire on forest structure and conclude that low intensity prescribed fires may reduce fuels without reducing "unnatural hierarchical clumping in the younger age classes of trees" (Bonnicksen and Stone 1981). Parsons and DeBenedetti (1979) describe the effects of fire suppression on several Sierran mixed conifer forest types. There is, however, little documentation of the effects of fire on long-term tree population dynamics. Understanding the causes, consequences, and variability of tree mortality and establishment is critical to predicting future changes in forest structure and composition (Franklin et al. 1987). These data are particularly important to ongoing efforts to model forest dynamics as part of a larger study of potential effects of climatic change on ecosystems of the southern Sierra Nevada (Stephenson and Parsons 1993, Miller 1994, Miller and Urban 1995).

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Fire history studies of mixed conifer forests indicate that fire was a frequent disturbance in these forests prior to European settlement (Kilgore and Taylor 1979, Swetnam et al. 1992, Swetnam 1993, Caprio and Swetnam 1995). For the period 1700 to 1900, mean fire intervals near our sites ranged from 7 to 10 yr, while two more mesic giant sequoia sites recorded mean fire intervals from 14 to 22 yr (Caprio and Swetnam 1995). The sudden end to this frequent, variable intensity fire regime in the late 19th century (linked to the introduction of intensive livestock grazing, elimination of Native American ignitions, and subsequently, organized fire suppression) (Vankat 1977, Kilgore and Taylor 1979, Swetnam et al. 1992, Swetnam 1993, Caprio and Swetnam 1995) resulted in the longest fire-free interval in these forests in at least the past 2,000 yr (Swetnam 1993). Fire exclusion has increased the density of the mixed conifer forest (Gibbens and Heady 1964, Kilgore 1973, Vankat 1977, Kilgore and Taylor 1979, Parsons and DeBenedetti 1979), dramatically reduced giant sequoia establishment (Stephenson 1994), and increased fuel load to hazardous levels (Parsons and DeBenedetti 1979, van Wagtendonk 1985).

In the late 1960s, the National Park Service began a program of prescribed burning to reduce the hazardous fuel buildup and to restore fire to its former role in mixed conifer forests (Bancroft et al. 1985). In 1990, the Tharp's Creek watershed was burned in a prescribed fire, providing the opportunity to compare mortality rates, changes in basal area and tree densities, and factors associated with mortality for a 5 yr pre-burn period and a 5 yr post-burn period between the burned Tharp's Creek watershed and the unburned Log Creek watershed. The questions we address in our study are: (1) What are mortality rates of trees by species and canopy class with and without prescribed fire? (2) How often are pathogens, insects, and fire-caused crown scorch associated with tree mortality, and what is the relationship between percent crown scorch and probability of tree mortality? (3) How do basal area and size structure change over a 5 yr period in burned versus unburned stands? (4) What are the differences between burned and unburned stands in numbers of ingrowth trees (trees reaching breast height over a 5 yr remeasurement period)?

Methods

Study Sites

The Log Creek and Tharp's Creek watersheds are located in the Giant Forest area of Sequoia National Park on the western slope of the southern Sierra Nevada of California. The Mediterranean climate of this region is characterized by wet, snowy winters and long, dry summers. Mean annual precipitation at Giant Forest, elevation 1950 m, is 1255 mm, and close to half of this falls as snow (Stephenson 1988) Mean January and July air temperatures at Giant Forest are 0°C and 18°C, respectively.

Study sites comprise the headwater drainages of Tharp's Creek (13.1 ha) and Log Creek (49.8 ha). Tharp's Creek is intermittent, typically running from November through June, while Log Creek is perennial. Soils of both the Tharp's and Log Creek watersheds are predominantly pachic xerumbrepts, derived from granodiorite (Huntington and Akeson 1987) Slopes are generally moderate to steep (6° to 29°). The aspect of Tharp's watershed ranges from south to southeast, and Log watershed aspect is primarily west to southwest and northwest. Elevations are 2097 to 2180 m in the Tharp's watershed and 2158 to 2371 m in the Log watershed.

Reference Stand Descriptions

A number of permanent forest reference stands were established in the 1980s in Sequoia National Park as part of an interdisciplinary, watershed-based National Park Service acid deposition research program—the plots were established to both describe the vegetation of the study watersheds and to provide a baseline against which to measure future change (Parsons et al. 1991). Two 1 ha reference stands representing the lower montane white fir-mixed conifer forest type (Rundel et al. 1977) were established in each of the Log Creek and Tharp's Creek watersheds. The reference stands were subjectively selected as being representative of the white fir-mixed conifer forest type, predominant in Giant Forest and in mid-elevation areas throughout the park. The Tharp's reference stands were established in 1984 and the Log reference stands in 1985. Following the methods used by Riegel et al. (1988), stands were surveyed along ordinal compass lines and slope-corrected, and all trees with heights ≥ 1.4 m were number-tagged and mapped by species and dbh.

Table 1 summarizes reference stand site characteristics and species composition. White fir (*Abies concolor*) predominates, and in all stands, shows the inverse J-shaped size distribution typical for shade-tolerant species (Leak 1975, Stewart 1986, Edmonds et al. 1993). Sugar pine (*Pinus lambertiana*) is most common in Lower Tharp's and Upper Log stands. Red fir (*Abies magnifica* [A. Murr.]), which is at the lower edge of its range in Giant Forest, is present in significant numbers only in the Lower Log stand. The northwestern aspect of this stand makes it a more favorable site for *A. magnifica* than the other three stands, which have more south- to southwest-facing aspects. Giant sequoia

Table 1. Site characteristics and 1985 species composition (relative density of species) for the four reference stands.

Reference stand	Elevational range (m)	Aspect	Slope (°)	ABCO	ABMA	PILA	SEGI	CADE	PIJE	QUKE
				(%)						
Lower Log	2133–2161	NW	6–18	77	21	2	1	0.2	—	—
Upper Log	2190–2207	SW	20–29	89	0.2	7	—	2	1	1
Lower Tharp's	2092–2126	S	10–22	80	1	17	0.2	0.2	1	0.2
Upper Tharp's	2154–2170	SE	9–25	96	—	2	—	—	2	—

NOTE: ABCO = *Abies concolor*, ABMA = *Abies magnifica*, PILA = *Pinus lambertiana*, SEGI = *Sequoiadendron giganteum*, CADE = *Calocedrus decurrens*, PIJE = *Pinus jeffreyi*, QUKE = *Quercus kelloggii*.

(*Sequoiadendron giganteum* [Lindl.] Buchh.), incense-cedar (*Calocedrus decurrens* [Torr.] Floren), Jeffrey pine (*Pinus jeffreyi* [Grev. and Balf.]), and black oak (*Quercus kelloggii* [Newb.]) are only minor components of these stands. Shrub cover ranges from 2% to 20% in the four reference stands, and the most common species are green manzanita (*Arctostaphylos patula* [Greene]), mountain whitethorn (*Ceanothus cordulatus* [Kell.]), chinquapin (*Chrysolepis sempervirens* [Kell.]) and gooseberry (*Ribes* spp.). Herbaceous vegetation contributes scattered cover; litter and duff form the predominant ground cover.

Determination of Tree Species Characteristics, Ingrowth, Mortality and Factors Associated with Mortality

In each reference stand, species, diameter at breast height (dbh) in cm, and canopy class (dominant, codominant, intermediate, and subcanopy) were recorded for each tree 1.4 m or more in height. Canopy classes were defined as follows: (1) Dominant—tree crown occupies space above the co-dominant canopy; (2) Co-dominant—tree crown is a component of the main stand overstory canopy; (3) Intermediate—tree crown extends both into and below the main stand overstory canopy; (4) Subcanopy—tree crown occupies space below the main stand overstory canopy (Parsons et al. 1992). Mortality was checked annually from 1986 to 1995 for each tree ≥1.4 m in height. Initial dbh measurements were done in 1985 in the Log Creek watershed and in 1984 in the Tharp's Creek watershed. We remeasured diameters and mapped ingrowth every 5 yr in the Tharp's stands (1984–1989 and 1989–1994), but due to time constraints, the remeasurement and ingrowth mapping interval for the Log stands was 7 yr (1985–1992). Ingrowth is defined as any tree that grew to breast height (1.4 m) in the remeasurement interval.

Signs and symptoms of pathogen and insect incidence were rated on three-point scales for each tree by trained observers when plots were established and for individual trees when they died (Parsons et al. 1992). We use the term *pathogen* to include fungi, bacteria, mycoplasma-like organisms, viruses, and parasitic flowering plants—all included in the definition of "biotic pathogen" by Tainter and Baker (1996). Signs included direct physical evidence such as fruiting bodies, larval galleries, mistletoe plant, or insects, while symptoms were physiological responses of trees (witches brooms, branch flagging or dieback, cankers). The three-point scales (in general terms) indicated 0—for no apparent signs or symptoms; 1—for light/moderate signs or symptoms; and 2—moderate/severe signs or symptoms. In this paper, we summarized incidence of disease and insects only in terms of presence or absence for all trees that died between 1985 and 1995.

Determination of Fire Effects on Stand Dynamics

The Tharp's prescribed burn was a 14 ha fire ignited October 23–26, 1990. Little activity was noted by October 28, but a few residual smokes lingered for several weeks. Due to low daytime relative humidity (21–30%), most of the ignition occurred early evenings and into the night shifts when relative humidity was 30–40%. Average fuel moistures for litter and duff were 28%, for 100 hr fuels 14%, and for 1000 hr fuels 64%. Air temperatures during ignition ranged from 10°C–16°C, and winds were calm. Fire behavior ranged from a backing fire with flame lengths of 0.05 to 0.15 m and rates of spread up to 0.1 m/min. to a strip headfire with flame lengths of 0.6 to 2.4 m (rate of spread not reported). Areas with heavy fuel concentrations and standing snags burned with the greatest severity, occasionally causing torching of nearby trees (Haggerty 1990). Total pre-burn fuel load was 210 Mg/ha and total reduction was 85%, the highest reduction occurring in litter/duff and 1 hr fuels (Table 2). Percent volume crown scorch was determined by ocular estimation for all trees in the Tharp's reference stands during spring and summer of 1991, the year after the fire.

We compared mean annual mortality rates for each species and canopy class between the Tharp's and Log reference stands for the periods 1986–1990 and 1991–1995 (5 yr prior to and 5 yr after Tharp's burn). For the two most abundant species, *A. concolor* and *P. lambertiana*, we used binary logistic regression (SPSS Inc. 1993) to model the probability of mortality after the Tharp's burn, using percent crown volume scorched (PCVS) and dbh as independent variables. The observed values of the dependent variable were 0 (live) or 1 (dead), and the probability of mortality (P_m) was estimated.

Because initial dbh measurements at the two watersheds were taken in different years and the Log stands had 7 rather than 5 yr as a remeasurement interval, the remeasurement intervals do not coincide perfectly between stands. Annual weather differences between the two periods resulted in differing growing conditions, thus it is not possible to make synchronous comparisons of basal area and size structure changes or ingrowth establishment for the two watersheds. Nonetheless, these data demonstrate how basal area and size class distributions change in burned versus unburned stands.

Table 2. Total fuel load pre- and post-burn and percent fuel reduction in 1990 Tharp's prescribed burn.

Fuel size	Pre-burn mean fuel load	Post-burn mean fuel load	Percent fuel reduction
	............(Mg/ha)............		
1-hr (0–0.6 cm)	5.15	0.16	96
10-hr (0.6–2.5 cm)	2.91	0.17	77
100-hr (2.5–7.5 cm)	6.73	2.69	60
1000-hr (>7.5 cm)			
(sound)	62.77	14.80	76
(rotten)	58.28	10.76	82
Litter/duff	73.98	2.24	97
Total	209.82	31.32	85

Results

Mortality Rates for Pre-Burn Period, 1986–1990

Log Creek Watershed

Mean annual mortality rates between 1986–1990 for trees ≥1.4 m tall were 1.0% and 0.5% for Lower Log and Upper Log, respectively (Tables 3 and 4). Rates were highest for the subcanopy trees in both stands (Figure 1a). No mortality occurred in the dominant canopy class during this period. For both reference stands combined, *A. magnifica* had the highest mean annual mortality rate (1.3%) for the 5 yr period, followed by *A. concolor* (0.7%), and *P. lambertiana* (0.6%). The mean annual mortality rate for all species in the watershed was 0.8%. Mortality affected *P. lambertiana* and *P. jeffreyi* approximately in proportion to their numbers in the watershed (Figure 2a). *A. concolor* was underrepresented and *A. magnifica* was overrepresented in total mortality relative to their numbers in the watershed.

Tharp's Creek Watershed

The mean annual mortality rate in Lower Tharp's was 0.8% and in Upper Tharp's 0.6% (Tables 5 and 6). The dominant and codominant canopy classes had the highest mortality rates in the Lower Tharp's stand, while the subcanopy class had similar mortality rates in both stands (Figure 1b). For the two stands together, the mean annual mortality rate of *P. lambertiana* was 1.2% and *A. concolor* 0.7% for the 5 yr period. The mean annual mortality rate for all species in the watershed was 0.8%, equal to that in the Log Watershed. *A. concolor* was underrepresented and *P. lambertiana* was overrepresented in total mortality relative to their numbers in the watershed (Figure 2a).

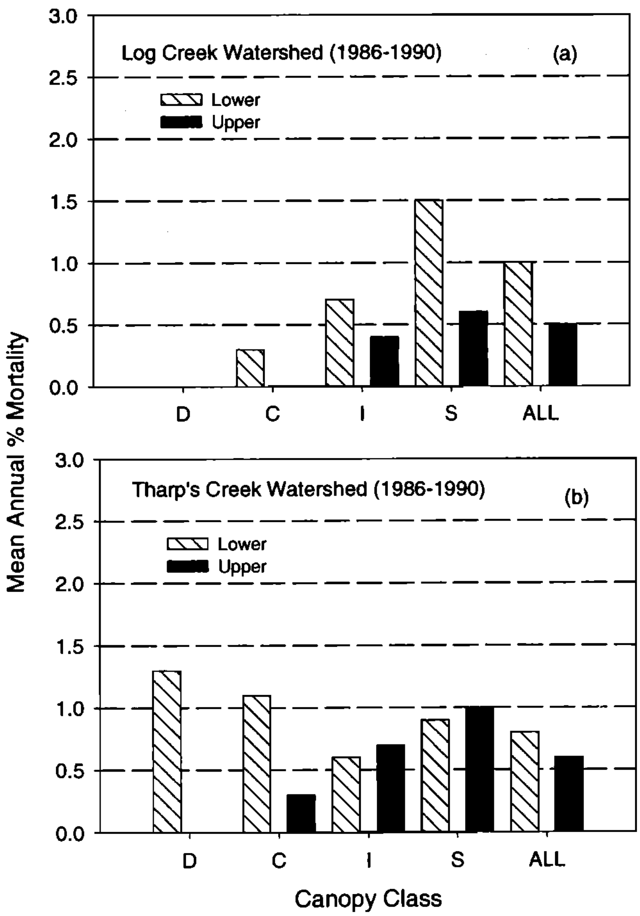

Figure 1. Mean annual percent mortality per canopy class within each reference stand between 1986-1990 for (a) Log Creek watershed stands, and (b) Tharp's Creek watershed stands. D = dominant, C = codominant, I = intermediate, S = subcanopy, and ALL includes trees from all canopy classes.

Mortality Rates for Post-Burn Period, 1991–1995

Log Creek Watershed

Mean annual mortality rates increased in both the Lower and Upper Log reference stands from 1986–1990 to 1991–1995 (Tables 3 and 4). Mortality rates increased in all canopy classes in the 1991–1995 period relative to the previous 5 yr period, with the exception of the dominant canopy class in Upper Log (Figures 1a and 3a). Mortality rates were highest in the codominant class in Upper Log (2.2%) and the subcanopy class in Lower Log (2.0%). *A. concolor* was underrepresented in total mortality relative to its presence in the watershed, while *A. magnifica* was overrepresented in percent mortality relative to its numbers in the watershed (Figure 2b). *A. concolor* increased in relative density between 1985 and 1995 by 2.2% and *A. magnifica* relative density decreased by 2.7%.

For both stands combined, *A. magnifica* had the highest mean annual mortality (4.7%) followed by *P. lambertiana* (1.2%) and *A. concolor* (1.1%). The mean annual mortality rate for all species in the watershed was 1.4%, an increase relative to the 0.8% mortality in the 1986–1990 period. Increased mortality rate in the Lower Log stand between 1986–1990 and 1991–1995 periods was due to the increase in *A. magnifica* mortality, while the increased mortality rate in the Upper Log stand was due to mortality increases in both *A. concolor* and *P. lambertiana* populations (Tables 3 and 4).

Tharp's Creek Watershed

The 1990 prescribed burn in the Tharp's Creek watershed resulted in a dramatic rise in mortality rates for 1991–1995 in both stands (Tables 5 and 6). The highest mortality rates occurred in the first post-burn year (35.2% and 49.4% for Lower and Upper Tharp's, respectively). Annual mortality rate declined to 2.6% in Lower Tharp's and 5.0% in Upper Tharp's by 1995. While these rates are still well above the 0.8% and 0.6% average annual mortality that occurred in the 5 yr pre-burn period, the 2.6% is within the range of annual mortality rates that occurred in the Log Creek watershed for this period. The Upper Tharp's stand generally had a wider range of annual mortality values than did the Lower Tharp's stand, reflecting the higher severity of burning in the upper stand.

The distribution of percent of total mortality among the different species in the watershed directly paralleled the species composition (Figure 2b). This is in contrast to the Log watershed, where large differences occurred between species composition and distribution of mortality among species (Figure 2a) between 1991 and 1995. The subcanopy class had the highest mean annual mortality in both stands (Figure 3b).

The mean annual mortality rate was 17.2% for all species in the Tharps watershed during the post-burn period. Among the more common species, mortality rates were similar: *P. jeffreyi*

Table 3. Populations and mortality of trees ≥ 1.4 m tall by species and canopy class for the Lower Log Creek reference stand, 1985–1995. Numbers and percentages are based on originally tagged trees (i.e., ingrowth is excluded).

Species and canopy class	Live trees/ha 1985	1990	1995	Mean annual percent mortality (and mortality range) 1986–1990	1991–1995
Abies concolor					
Dominant	10	10	9	**0.0**	**1.8** (0.0–9.1)
Codominant	36	35	35	**0.5** (0.0–2.5)	**0.0**
Intermediate	91	89	86	**0.4** (0.0–1.0)	**0.6** (0.0–1.0)
Subcanopy	174	163	154	**1.4** (0.0–2.6)	**1.0** (0.0–1.7)
All classes	311	297	285	**1.0** (0.0–2.3)	**0.8** (0.3–1.2)
Abies magnifica					
Dominant	4	4	4	**0.0**	**0.0**
Codominant	15	15	11	**0.0**	**3.8** (0.0–6.7)
Intermediate	36	33	29	**1.5** (0.0–5.0)	**2.2** (0.0–5.7)
Subcanopy	28	26	14	**1.8** (0.0–5.9)	**9.5** (0.0–27.6)
All Classes	83	78	58	**1.2** (0.0–4.1)	**4.7** (0.0–11.5)
Pinus lambertiana					
Intermediate	4	4	4	**0.0**	**0.0**
Subcanopy	3	3	3	**0.0**	**0.0**
All classes	7	7	7	**0.0**	**0.0**
Sequoiadendron giganteum					
Codominant	2	2	2	**0.0**	**0.0**
Intermediate	1	1	1	**0.0**	**0.0**
Subcanopy	2	2	2	**0.0**	**0.0**
All classes	5	5	5	**0.0**	**0.0**
Calocedrus decurrens					
Subcanopy	1	1	1	**0.0**	**0.0**
All classes	1	1	1	**0.0**	**0.0**
All species					
Dominant	14	14	13	**0.0**	**1.3** (0.0–6.3)
Codominant	53	52	48	**0.3** (0.0–1.7)	**1.1** (0.0–1.8)
Intermediate	132	127	120	**0.7** (0.0–2.1)	**1.0** (0.0–2.2)
Subcanopy	208	195	174	**1.5** (0.0–3.1)	**2.0** (0.5–5.0)
All classes	405	387	354	**1.0** (0.0–2.2)	**1.5** (0.2–3.2)

(19.7%), *A. concolor* (17.1%), and *P. lambertiana* (16.1%). All species except *C. decurrens* and *S. giganteum* showed an increase in mortality in the post-burn period.

Factors Associated with 1986–1990 Mortality

Branch-flagging (or displaying of dead brown branches amidst an otherwise green crown) occurred on approximately one-half of trees that died; this can be symptomatic of white pine blister rust on sugar pine, fir canker (*Cytospora abietis*), and a number of other fungal diseases of conifers (Bega and Scharpf 1993, Scharpf 1993). Dwarf mistletoe was the most common pathogen associated with the fir trees that died between 1986 and 1990 in the Log Creek watershed (Table 7). Fir canker was the next most common. The latter is a weak parasite that only attacks trees previously stressed by other disease-causing agents, drought, fire, insects, or human activities (Scharpf 1993). White pine blister rust is common in the Giant Forest study area, but it occurred at very low frequency in the reference stands (Parsons et al. 1992) (Table 7). Of the six types of insects surveyed, the fir engraver was the only one found to be associated with any trees that died during this 5 yr period.

Factors Associated with Mortality, 1991–1995

In the Log Creek watershed, dwarf mistletoe and fir canker were associated with a high percentage of the dead *A. magnifica* and a smaller percentage of the dead *A. concolor* (Table 8). Fir engravers were the most important insect associated with mortality. A small percentage of mortality (2%) due to stem/root failure was identified in the white fir population, and crushing by another tree killed a much larger percentage of trees than in the previous 5 yr period.

The mortality in the Tharp's Creek watershed stands was most directly related to fire-caused crown scorch (Table 8). For *A. concolor*, logistic regression indicated that probability of mortality in the 5 yr post-burn period was positively correlated ($P < 0.001$) with percent crown volume scorched (PCVS) and negatively correlated with dbh ($P < 0.002$). The probability of mortality follows a positive logistic curve for PCVS and a negative trend (although with weak correlation) for dbh. In contrast, dbh was not significantly correlated with probability of survival in *P. lambertiana*. Thus, probability of mortality in *P. lambertiana* was modeled using only percent crown scorch; similar to *A. concolor*, there was a significant

Table 4. Populations and mortality of trees ≥1.4 m tall by species and canopy class for the Upper Log Creek reference stand, 1985–1995. Numbers and percentages are based on originally tagged trees (i.e., ingrowth is excluded).

Species and	Live trees/ha			Mean annual percent mortality (and mortality range)	
canopy class	1985	1990	1995	1986–1990	1991–1995
Abies concolor					
Dominant	3	3	3	**0.0**	**0.0**
Codominant	48	48	42	**0.0**	**2.6** (0.0–8.7)
Intermediate	126	125	120	**0.3** (0.0–0.8)	**0.8** (0.0–1.6)
Subcanopy	190	184	173	**0.7** (0.0–2.1)	**1.3** (0.6–2.8)
All classes	367	360	338	**0.5** (0.0–1.4)	**1.3** (0.6–2.9)
Abies magnifica					
Subcanopy	1	1	1	**0.0**	**0.0**
All classes	1	1	1	**0.0**	**0.0**
Pinus lambertiana					
Dominant	1	1	1	**0.0**	**0.0**
Codominant	5	5	5	**0.0**	**0.0**
Intermediate	7	6	5	**2.9** (0.0–14.3)	**3.3** (0.0–16.7)
Subcanopy	14	14	13	**0.0**	**1.4** (0.0–7.1)
All classes	27	26	24	**0.7** (0.0–3.7)	**1.5** (0.0–7.7)
Pinus jeffreyi					
Codominant	2	2	2	**0.0**	**0.0**
Intermediate	0	0	0	—	—
Subcanopy	3	3	3	**0.0**	**0.0**
All classes	5	5	5	**0.0**	**0.0**
Calocedrus decurrens					
Intermediate	3	3	3	**0.0**	**0.0**
Subcanopy	7	7	7	**0.0**	**0.0**
All classes	10	10	10	**0.0**	**0.0**
Quercus kelloggii					
Intermediate	1	1	1	**0.0**	**0.0**
Subcanopy	2	2	2	**0.0**	**0.0**
All classes	3	3	3	**0.0**	**0.0**
All species					
Dominant	4	4	4	**0.0**	**0.0**
Codominant	55	55	49	**0.0**	**2.2** (0.0–7.5)
Intermediate	137	134	128	**0.4** (0.0–1.5)	**0.9** (0.0–1.5)
Subcanopy	218	211	198	**0.6** (0.0–1.8)	**1.3** (0.5–1.9)
All classes	413	405	381	**0.5** (0.0–1.2)	**1.3** (0.5–3.1)

($P < 0.003$) and positive correlation between percent crown volume scorched and probability of survival. Tests of significance (–2 log likelihood, SPSS 1993) indicated $P < 0.001$ for both *A. concolor* and *P. lambertiana* regression models (Table 9).

Dwarf mistletoe and fir engravers on *A. concolor* and white pine blister rust on *P. lambertiana* were found on similar percentages of trees that died and trees that survived the fire. Therefore, there is no indication that there was a relationship between pre-existing disease or insect conditions and fire-induced mortality.

Changes in Basal Area and Size Structure

A. concolor contributed the largest proportion of the total initial basal area in both Log Creek stands (70% in Lower Log and 84% in Upper Log). In the Lower Log stand, *A. magnifica* contributed most of the remainder of total basal area, while *P. lambertiana* was the second most important contributor in the Upper Log stand. The average annual percent change in basal area was similar in both stands between 1985 and 1992 (+0.84% in Lower Log and +0.80% in Upper Log) (Table 10).

Lower Tharp's had a slight decline in total basal area between 1984 and 1989 (0.06 m^2 ha^{-1}, or about 0.01%/yr), due primarily to the death of numerous codominant and intermediate *A. concolor* trees. Upper Tharp's had an increase in basal area during this period (2.45 m^2 ha^{-1}, or 0.61%/yr). Between 1989 and 1994, both stands had a large decline in total basal area, primarily due to fire-related mortality. Total basal area decreased by 20.21 m^2 ha^{-1} (or 4.71%/yr) in Lower Tharp's, and by 25.53 m^2 ha^{-1} (or 6.19%/yr) in Upper Tharp's (Table 11).

The most significant change in size structure that occurred in the Log watershed between 1985 and 1992 was in the smallest size class (Figures 4a and b). The decrease in numbers of trees in the smallest size class reflects the relatively high mortality rate in this size class, compared to the

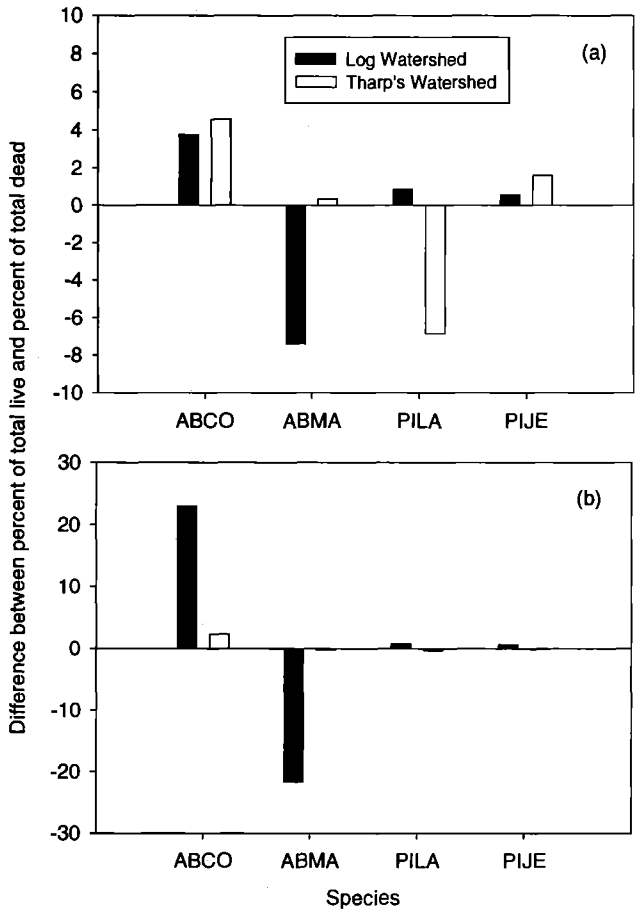

Figure 2. The relative percent of total live trees represented by each species at the beginning of each measurement period minus the relative percent of total dead trees at the end of the measurement period for the same species for (a) 1986–1990 measurement period and (b) 1991–1995 measurement period. ABCO = *Abies concolor*, ABMA = *Abies magnifica*, PILA = *Pinus lambertiana*, and PIJE = *Pinus jeffreyi*.

larger size classes. Even with the inclusion of 1985–1992 ingrowth, there was still a decline of an average of 14 trees/ha in this size class.

In contrast, there was a dramatic change in the size structure of the Tharp's watershed between 1989 and 1994 (Figures 4c and d). The mean number of trees/ha declined in most size classes. Seventy-five percent of the trees ≤50 cm dbh were killed, and 25% of the trees >50 cm dbh were killed.

Ingrowth Establishment

For the Log watershed 1985–1992 period, there was a total of 28 ingrowth trees—16 *A. concolor*, 10 *A. magnifica*, 1 *P. lambertiana*, and 1 *C. decurrens*. The mean annual ingrowth rates for the Log Creek watershed for this period were as follows: *A. concolor* (0.3%), *A. magnifica* (1.7%), *P. lambertiana* (0.4%), and *C. decurrens* (1.2%). For the 1984–1989 period in the Tharp's watershed, we noted 12 ingrowth trees. Lower Tharp's had 6 *A. concolor*, and Upper Tharp's had 4 *A. concolor* and 2 *P. lambertiana*. The mean annual ingrowth rates for the Tharp's Creek watershed for this period were: *A. concolor* (0.3%) and *P. lambertiana* (0.5%).

For the 1989–1994 period in the Tharp's Creek watershed, we observed only three ingrowth trees. They were all in Lower Tharp's: one each of *A. concolor*, *A. magnifica*, and *Q. kelloggii*. Some of the potential ingrowth for this last period was probably killed by the 1990 prescribed burn prior to the 1994 remeasurement year, and 9 out of the 12 ingrowth trees for the 1984–1989 period were killed by the Tharp's burn. All were *A. concolor*.

Discussion

Mortality Causes and Implications

1986–1990

The highest mortality rates occurred in the subcanopy or intermediate canopy classes. Preliminary examination of tree-ring samples collected from dead trees in the Lower Log Creek stand indicated that these trees often had low growth rates for years to decades prior to their deaths (unpublished data). Suppression has been suggested as a major cause of tree death in similar studies of tree mortality in the Pacific Northwest (Edmonds et al. 1993, DeBell and Franklin 1987). We speculate that suppression was the ultimate cause of mortality in most subcanopy and many intermediate class trees. Proximate causes were a higher proportion of stress symptoms which may lead to mortality (physical deformities, pathological characteristics, and insect incidence) relative to trees in more dominant canopy classes (Parsons et al. 1992).

While insects and pathogens have long been vital parts of dynamic forests, their incidence has most likely increased (relative to the pre-Euro-American settlement period) due to the higher forest densities resulting from many decades of fire suppression (Kilgore 1973, Savage 1994, Ferrell 1996). More trees in dense forests are susceptible to insect and pathogen attack because there is increased competition for resources, particularly during extended drought. Higher tree densities also increase the opportunities for insect and pathogen dispersal (Kilgore 1973, Swetnam and Lynch 1993, Ferrell 1996).

In both the white fir and red fir populations, dwarf mistletoe was the most common pathogen associated with mortality, and the fir canker *C. abietis* was found on most of the *A. magnifica* infected with mistletoe. Scharpf (1993) reports that dwarf mistletoe is one of the most important factors predisposing *Abies* to attack by *C. abietis*. The prevalence of mistletoe in our reference stands is consistent with results from statewide mistletoe surveys. Throughout California, mistletoe is prevalent in about 30% of *A. concolor* stands and about 50% of *A. magnifica* stands (Scharpf and Hawksworth 1993).

Fir engravers were the only bark insects associated with mortality, being noted on *A. concolor* in both Log and Tharp's Creek watersheds. In a recent study in the Sierra Nevada at Lake Tahoe nearly all *A. concolor* sampled in six study stands had been attacked by fir engravers, and between 1987–1989, 36.3% of the 633 firs sampled had been killed or were dying from fir engraver attack (Ferrell et al. 1994). In that study, the highest basal area stands with a large component of *A. concolor* suffered the greatest mortality. Widespread drought stress also contributed to the high mortality (Ferrell et al. 1994).

Table 5. Populations and mortality of trees ≥1.4 m tall by species and canopy class in the Lower Tharp's reference stand, 1985–1995. Numbers and percentages are based on originally tagged trees (i.e., ingrowth is excluded).

Species and canopy class	Live trees/ha 1985	Live trees/ha 1990	Live trees/ha 1995	Mean annual percent mortality (and mortality range) 1986–1990	Mean annual percent mortality (and mortality range) 1991–1995
Abies concolor					
Dominant	8	8	5	**0.0**	**7.0** (0.0–22.2)
Codominant	87	83	61	**1.2** (0.0–3.1)	**5.5** (2.6–8.3)
Intermediate	125	121	57	**0.7** (0.0–1.4)	**13.7** (3.1–29.4)
Subcanopy	155	149	17	**0.7** (0.0–1.7)	**30.7** (5.6–70.0)
All classes	375	361	140	**0.8** (0.0–1.4)	**16.4** (3.1–37.0)
Abies magnifica					
Subcanopy	2	2	0.0	**0.0**	**55.6** (0.0–100.0)
All classes	2	2	0.0	**0.0**	**55.6** (0.0–100.0)
Pinus jeffreyi					
Dominant	1	1	1	**0.0**	**0.0**
Codominant	2	2	1	**0.0**	**10.0** (0.0–50.0)
Intermediate	0	0	0	**0.0**	**0.0**
Subcanopy	3	3	0	**0.0**	**100.0** (N/A)
All classes	6	6	2	**0.0**	**16.7** (0.0–50.0)
Pinus lambertiana					
Dominant	4	3	3	**5.0** (0.0–25.0)	**0.0**
Codominant	11	11	7	**0.0**	**7.5** (0.0–18.2)
Intermediate	30	30	12	**0.0**	**14.6** (0.0–42.9)
Subcanopy	38	34	4	**1.9** (0.0–4.9)	**26.8** (0.0–71.4)
All classes	83	78	26	**1.1** (0.0–2.2)	**17.2** (0.0–46.0)
Calocedrus decurrens					
Intermediate	1	1	1	**0.0**	**0.0**
Subcanopy	0	0	0	—	—
All classes	1	1	1	**0.0**	**0.0**
Quercus kelloggii					
Subcanopy	1	1	0	**0.0**	**50.0** (0.0–100.0)
All classes	1	1	0	**0.0**	**50.0** (0.0–100.0)
Sequoiadendron giganteum					
Dominant	1	1	1	**0.0**	**0.0**
All classes	1	1	1	**0.0**	**0.0**
All species					
Dominant	15	14	11	**1.3** (0.0–6.7)	**4.5** (0.0–14.3)
Codominant	113	107	79	**1.1** (0.0–1.8)	**5.9** (2.5–8.5)
Intermediate	176	171	78	**0.6** (0.0–1.2)	**13.8** (2.5–31.9)
Subcanopy	226	216	21	**0.9** (0.0–2.7)	**28.2** (4.3–64.8)
All classes	469	450	170	**0.8** (0.0–1.7)	**16.7** (2.6–35.2)

The pathogen with most potential for causing high mortality in pines is the introduced white pine blister rust that infects five-needled pines, including *P. lambertiana*. White pine blister rust is not yet prevalent in these four reference stands, but it has been a frequent cause of mortality in *P. lambertiana* in other areas in Sequoia National Park (unpublished data). White pine blister rust has been identified as a factor contributing to the changing forest composition of mixed conifer stands in the Sierra Nevada, due to its role in reducing the frequency of *P. lambertiana* (Byler and Parmeter 1979).

Between 1986 and 1990, annual mortality rates in both watersheds (ranging from 0 to 2.2%) were within the range of what might be expected due to self-thinning in the absence of major disturbance (Mohler et al. 1978, Harcombe and Marks 1983, Waring and Schlesinger 1985). Mean annual mortality rates of 0.8% for both the Log watershed and the Tharp's watershed between 1986 and 1990 were similar to mortality rates reported for old-growth forests in the Olympic Mountains in Washington for this same time period (Edmonds et al. 1993).

1991–1995

Mortality in the Log Creek watershed was generally more evenly distributed among the intermediate, codominant, and dominant size classes in the 1991–1995 sampling period than during the previous 5 yr. It is possible that drought stress may be more severe in older, less vigorous trees (Elliott and Swank 1994) and may have contributed to the increase in mortality in the larger canopy classes during the latter period, during and following the 1987–1992 drought.

The effects of extreme climatic events, such as drought, on tree vigor are likely to be more acute when accompanied by such anthropogenic disturbances as air pollution or fire suppression (Savage 1994). The high levels of ozone that have been recorded in recent years for the southern Sierra Nevada are known to produce visible foliar injury, premature needle abscission (Duriscoe and Stolte 1989), and growth reduction (Peterson et al. 1987), and to affect photosynthetic rates and stomatal conductance in *P. jeffreyi* (Patterson and Rundel 1989). In many cases, pollution weakens trees without being a direct cause of death (Savage 1994). These stresses are often coupled with increases in forest density

Table 6. Populations and mortality of trees ≥1.4 m tall by species and canopy class in Upper Tharp's reference stand, 1985–1995. Numbers and percentages are based on originally tagged trees (i.e., ingrowth is excluded).

Species and canopy class	Live trees/ha 1985	1990	1995	Mean annual percent mortality (and mortality range) 1986–1990	1991–1995
Abies concolor					
Dominant	34	34	20	**0.0**	**9.8** (0.0–16.7)
Codominant	76	75	49	**0.3** (0.0–1.3)	**8.1** (1.1–14.7)
Intermediate	108	105	31	**0.6** (0.0–1.9)	**19.5** (3.1–46.7)
Subcanopy	120	114	8	**1.0** (0.0–2.6)	**28.0** (0.0–86.8)
All classes	338	328	108	**0.6** (0.0–1.5)	**17.8** (5.3–50.0)
Pinus jeffreyi					
Dominant	1	1	1	**0.0**	**0.0**
Codominant	1	1	0	**0.0**	**33.3** (0.0–100.0)
Intermediate	2	2	1	**0.0**	**10.0** (0.0–50.0)
Subcanopy	4	4	0	**0.0**	**87.5** (75.0–100.0)
All classes	8	8	2	**0.0**	**21.7** (0.0–50.0)
Pinus lambertiana					
Codominant	1	1	0	**0.0**	**33.3** (0.0–100.0)
Intermediate	4	3	2	**5.0** (0.0–25.0)	**6.7** (0.0–33.3)
Subcanopy	2	2	1	**0.0**	**10.0** (0.0–50.0)
All classes	7	6	4	**2.9** (0.0–14.3)	**11.7** (0.0–33.3)
All species					
Dominant	35	35	21	**0.0**	**9.5** (0.0–14.3)
Codominant	78	77	49	**0.3** (0.0–1.3)	**8.6** (2.0–14.3)
Intermediate	114	110	35	**0.7** (0.0–1.8)	**18.5** (2.8–45.5)
Subcanopy	126	120	9	**1.0** (0.0–2.4)	**27.9** (0.0–85.8)
All classes	353	342	113	**0.6** (0.0–1.4)	**17.7** (5.0–49.7)

resulting from fire suppression (Kilgore 1973, Kilgore and Taylor 1979, Parsons and DeBenedetti 1979, Swetnam et al. 1992). The increases in density have resulted in increased competition for limited soil moisture in this summer-dry climate (Arkley 1981). Piirto (1977) suggests that increased densities of shade-tolerant white fir in the absence of fire result in an increase in the amount of Annosus root disease (*Heterobasidion annosum* [Fr.] Bref.) (a major pathogen causing root and butt rot in many tree species) inoculum in mixed conifer stands and in the likelihood of pathogen spread through root grafts.

We speculate that moisture stress greatly increased the susceptibility of *A. magnifica* to pathogen and insect-related mortality. The relatively high mortality rate of *A. magnifica* correlates with the extended drought in the southern Sierra Nevada from 1987–1992. The optimal elevational range of *A. magnifica* in this region is 2,130 to 2,745 m (Oosting and Billings 1943). Between the extremes of its elevational distribution, it occurs in extensive, almost pure stands. At the lower end of its elevational range (as in Giant Forest), *A. magnifica* must compete with species such as *A. concolor*, *P. lambertiana*, and *S. giganteum*, which are well within their optimal elevational ranges and are presumably better adapted to sustain themselves during drought conditions at these elevations. The decline in relative density of *A. magnifica* during this period (–2.7%) may be somewhat compensated for by the higher establishment rate of *A. magnifica* relative to *A. concolor* in these stands (see *Ingrowth Establishment* section under *Results*).

Mistletoe, fir cankers, and fir engravers were commonly associated with dead fir trees, and mistletoe and fir cankers were particularly prevalent in the *A. magnifica* population. The increased percentage of trees dying from root or stem failure and crushing during this period illustrated the effect that a high precipitation year can have on mortality in some stands. The winter of 1994–1995 was a high precipitation year (175% of the 1926–1991 average). The combination of increased snow and wind from storms contributed to the failure of several large trees in or near the Upper Log stand, which in turn crushed a number of smaller trees.

Crown scorch was the predominant mortality cause in the Tharp's watershed. Similar percentages of dead and still-living trees had dwarf mistletoe, white pine blister rust, and fir engravers associated with them. It is unlikely that the presence of these conditions made trees more susceptible to fire mortality because similar percentages of trees that survived the fire have the same characteristics. It is also possible that fine root mortality played a role in the death of trees several years after the fire, as burning has been shown to reduce fine root biomass up to 50 to 75% in *Pinus ponderosa* Laws. (Grier 1989, Swezy and Agee 1991). Our initial fuel loads (210 Mg/ha) were much higher than those reported by Grier (1984)—85 Mg/ha—and the 97% reduction in litter and duff that we found in our burn suggests that the fire burned with relatively high severity in terms of its residence time and consumption of the fuel layer closest to the upper layer of soil where most fine roots occur.

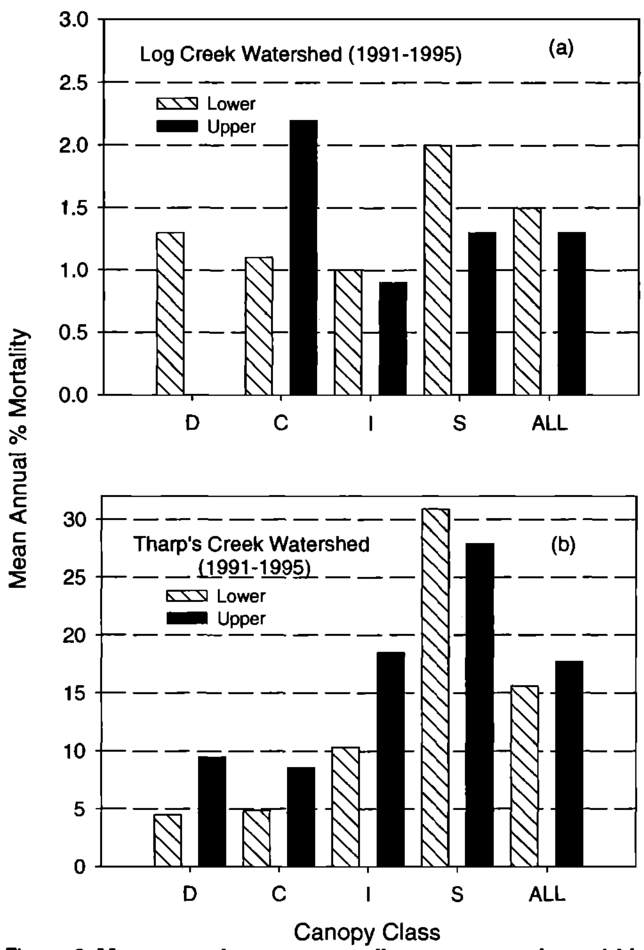

Figure 3. Mean annual percent mortality per canopy class within each reference stand between 1991–1995 for (a) Log Creek watershed stands, and (b) Tharp's Creek watershed stands. D = dominant, C = codominant, I = intermediate, S = subcanopy, and ALL includes trees from all canopy classes. Note differences in scales.

A. concolor, *A. magnifica*, and *C. decurrens* are particularly fire-susceptible in small diameter classes, due to their low branches and thin bark. *P. lambertiana* also has thin, dense bark that insulates the cambium poorly against heat damage (Wagener 1961). Adult *P. jeffreyi*, with thick bark and high crowns, are typically the most well-adapted to fire of all species in these stands, aside from *S. giganteum*.

Although species do have variable tolerances to fire, it appears that fire (especially high severity fire, or fire that has a high impact on the site as a function of both its intensity and its residence time at the site) is a more generally effective agent of mortality than are disease, drought, insects, air pollution, and other factors associated with mortality, which tend to have more species-specific impacts. Thus, the proportion of fire-caused mortality among species tends to reflect the species' relative occurrences in the watershed.

The initially high post-burn mortality rates of 35.2% and 49.4% in Lower and Upper Tharp's in 1991 declined to 2.6 and 5.0%, respectively, by 1995. Mortality rates should continue to decline in the next several years until they reach near pre-burn levels. The more rapid decline in mortality rates in Upper Tharp's compared to Lower Tharp's may be due to the fact that trees were more severely scorched in the Upper Tharp's stand, resulting in more mortality in the first post-burn year relative to Lower Tharp's. Lower amounts of crown scorch in the Lower Tharp's stand may have delayed mortality an additional year or two for many trees. Delayed mortality in trees with lower crown scorch may have been related to fine root mortality from duff consumption. Low heating over a long period of time is sufficient to kill shallow roots (Hare 1961). The higher fire severity and scorching in Upper Tharp's probably contributed to the higher mortality in the codominant and dominant canopy classes in that stand

Table 7. Numbers and percentages (calculated as percent of total dead trees per species) of trees that died between 1986 and 1990 in the Log and Tharp's watersheds that were associated with branch-flagging or the listed diseases and/or insects at the time of plot establishment. The last two categories (root/stem failure or crushing) were noted at the year of tree death. Percentages in each column add up to greater than 100% because mortality for any given tree may be associated with more than one contributing factor.

Factors associated with mortality	ABCO	ABMA	PILA
	Total (%)		
Log Creek Watershed			
Branch-flagging	5 (21%)	5 (83%)	1 (100%)
Dwarf mistletoe (*Arceuthobium* spp.)	9 (38%)	5 (83%)	0
Fir canker (*Cytospera abietis*)	0	4 (67%)	—
Fir engraver (*Scolytus ventralis*)	4 (17%)	0	—
Root or stem failure	0	0	0
Crushing by another tree	2 (8%)	0	0
Total dead	24	6	1
Tharp's Creek Watershed			
Branch-flagging	6 (22%)	—	4 (67%)
Dwarf mistletoe (*Arceuthobium* spp.)	0	—	1 (17%)
Indian paint fungus (*Echinodontium tinctorium*)	1 (4%)	—	0
White pine blister rust (*Cronartium ribicola*)	0	—	2 (33%)
Fir engraver (*Scolytus ventralis*)	7 (26%)	—	—
Root or stem failure	1 (4%)	—	0
Crushing by another tree	2 (7%)	—	0
Total dead	27	—	6

Table 8. Numbers and percentages (calculated as percent of total dead trees per species) of trees that died between 1991 and 1995 in the Log and Tharp's watersheds and were associated with branch-flagging, crown scorch ≥50% (Tharp's only), or the listed diseases and/or insects. Percentages in each column add up to greater than 100% because mortality for any given tree may be associated with more than one contributing factor.

Factors associated with mortality	ABCO	ABMA	PILA	PIJE
	··········Total (%)··········			
Log Creek Watershed				
Branch-flagging	10 (27%)	12 (57%)	0	—
Dwarf mistletoe	15 (41%)	17 (81%)	0	—
Indian paint fungus	2 (3%)	0	—	—
Fir canker (*Cytospera abietis*)	4 (11%)	9 (43%)	—	—
Fir engraver	7 (19%)	3 (14%)	—	—
Root or stem failure	2 (5%)	0	0	—
Crushing by another tree	13 (35%)	1 (5%)	2 (100%)	—
Total dead	37	21	2	0
Tharp's Creek Watershed				
Branch flagging	54 (12%)	1 (50%)	26 (43%)	4 (40%)
Dwarf mistletoe	53 (12%)	0	0	0
Indian paint fungus	5 (1%)	0	—	—
Red belt fungus (*Fomitopsis pinicola*)	0	0	1 (2%)	0
White pine blister rust	—	—	8 (13%)	—
Pine beetles (*Dendroctonus* spp.)	—	—	3 (5%)	1 (10%)
Fir engraver	146 (31%)	0	—	—
Crushing by another tree	3 (0.4%)	0	0	0
Scorch >50%	409 (87%)	1 (50%)	43 (69%)	8 (80%)
Total dead	468	2	61	10

NOTE: One black oak died during this period in the Tharp's Creek Watershed, but it did not have any of the above factors associated with it other than ≥50% scorch.

and the wider range of annual mortality values observed in Upper Tharp's relative to Lower Tharp's.

It is unclear why dbh was not significantly correlated with survival in the logistic regression for *P. lambertiana*. Stephens (1995) also used logistic regression to model probability of survival as a function of dbh and percent crown volume scorched (PCVS) for *A. concolor* and *P. lambertiana*. He found dbh and PCVS to be significant predictors of mortality for both species. The lack of dbh significance in our model for *P. lambertiana* could be related to lower sample sizes as well as a wider range of dbh values. Stephens' sample size was 140 and his range of dbh values 5–60 cm, while our sample size was 93 and range of dbh values 0.5–156 cm. We also had many small diameter trees in our plots (68% of the *P. lambertiana* are less than 20 cm dbh), and these trees frequently sustained 100% crown scorch. If we had had a larger sample size of medium to large diameter trees, a significant relationship might have resulted between diameter and mortality in our model.

Table 9. Summary of logistic regression equations for *A. concolor* and *P. lambertiana* mortality after fire. P_m = probability of mortality, PCVS = Percent Crown Volume Scorch, and DBH = Diameter at Breast Height (cm).

Species	Logistic regression equation
A. concolor	$P_m = 1/1+[e^{-(-1.4197+0.0524\,PCVS-0.0141\,DBH)}]$
	$\chi^2 = 545.83$, df = 2, $P < 0.001$
P. lambertiana	$P_m = 1/1+[e^{-(-1.1512+0.1074\,PCVS)}]$
	$\chi^2 = 63.34$, df = 1, $P < 0.001$

Changes in Basal Area and Size Structure

The initial basal area totals for these stands were within the range of basal areas found in old-growth forests in Oregon and Washington (Grier and Logan 1977, Franklin and DeBell 1988, Edmonds et al. 1993), were somewhat lower than basal areas reported by Parsons and DeBenedetti (1979) and higher than basal areas reported by Vankat and Major (1978) and Rundel et al. (1977) for Sierran white fir-mixed conifer forests. When mortality was concentrated in the lower canopy classes (or smaller diameter trees), the total basal area increased an average of 0.6–0.8% per year. Higher mortality rates in codominant and dominant classes resulted in a slightly declining basal area in Lower Tharp's for the first 5 yr period.

The large reductions in tree densities and basal areas resulting from the Tharp's burn will provide more opportunities for successful establishment of less shade-tolerant species and will help reduce fuel inputs, presumably reducing the hazard of uncontrollable wildfire in this watershed (Kilgore 1973, Stephenson et al. 1991, van Wagtendonk 1996). According to van Wagtendonk (1996), prescribed burning appears to be the most effective treatment for reducing a subsequent fire's rate of spread, fireline intensity, flame length, and heat per unit area. Efforts to model interactions of forest dynamics and disturbance regime have emphasized the importance of reducing basal area in prescribed burns that have fuel reduction as an objective (Miller 1994). Burns which do not significantly reduce the number of trees in dense stands

Table 10. Basal area (BA) and average annual percent change in basal area for each species in the Lower Log and Upper Log reference stands, 1985–1992. These numbers include only originally tagged trees (i.e., ingrowth is excluded).

	BA (m^2/ha)		Average annual percent change BA/yr
Species	1985	1992	(1985–1992)
Lower Log Reference Stand			
A. concolor	47.98	50.46	1.03
A. magnifica	18.73	18.89	0.17
P. lambertiana	0.66	0.71	1.52
S. giganteum	1.23	1.42	3.09
C. decurrens	0.00	0.00	0.00
Stand total	68.60	71.48	
Stand average			0.84
Upper Log Reference Stand			
A. concolor	45.02	46.67	0.73
A. magnifica	0.00	0.00	0.00
P. lambertiana	7.39	7.87	1.30
P. jeffreyi	0.54	0.55	0.37
C. decurrens	0.88	0.90	0.45
Q. kelloggii	0.05	0.05	0.00
Stand total	53.88	56.04	
Stand average			0.80

will not be successful in long-term fuel reduction, since high basal area stands have high fuel input rates (Miller 1994). Keifer (1995) reports that woody fuel may increase to near pre-burn levels in the white fir and giant sequoia types 5 to 10 yr following prescribed fire.

While the Tharp's burn reduced fuels and basal area substantially, future burns will be necessary to maintain reduced tree densities and low fuel accumulation rates. The rapid accumulation of woody fuels in the first 5 yr after a fire is due to the fire-caused death of small trees in the abnormally dense thickets which have become established in the absence of frequent fires (Parsons 1978) and the limb-dropping and falling of larger trees that may die more slowly due to a combination of fire-, pathogen- and insect-related causes post-burn. A sustained reduction of fuel accumulation rates to their probable levels at the time prior to Euro-American settlement will require at least two prescribed fires, the second of which removes the woody fuel accumulation from fire-caused tree mortality (Stephenson 1996).

Ingrowth Establishment

Ingrowth establishment was more successful in the Log Creek watershed than in the Tharp's Creek watershed for the pre-burn measurement periods. Although the measurement periods are not synchronous between the two watersheds, there is some overlap between the two (1985–1989), and climatic

Table 11. Basal area (BA) and average annual percent change in basal area for each species in the Lower Tharp's and Upper Tharp's reference stands, 1984–1989 and 1989–1994. These numbers include only originally tagged trees (i.e., ingrowth is excluded).

	BA (m^2/ha)			Average annual percent change BA/yr	
Species	1984	1989	1994	(1984–1989)	(1989–1994)
Lower Tharp's Reference Stand					
A. concolor	64.78	64.45	48.42	–0.10	–4.97
A. magnifica	0.01	0.01	0.00	0.00	0.00
P. lambertiana	15.42	15.55	12.22	0.17	–4.28
P. jeffreyi	3.01	2.97	2.01	0.27	–6.46
S. giganteum	2.52	2.68	2.80	1.27	0.90
C. decurrens	0.13	0.15	0.17	3.08	2.67
Stand total	85.89	85.83	65.62		
Stand average				–0.01	–4.71
Upper Tharp's Reference Stand					
A. concolor	77.57	79.94	55.84	0.60	–6.03
P. lambertiana	0.56	0.60	0.13	1.39	–15.67
P. jeffreyi	1.88	1.92	0.96	0.42	–10.00
Stand total	80.01	82.46	56.93		
Stand average				0.61	–6.19

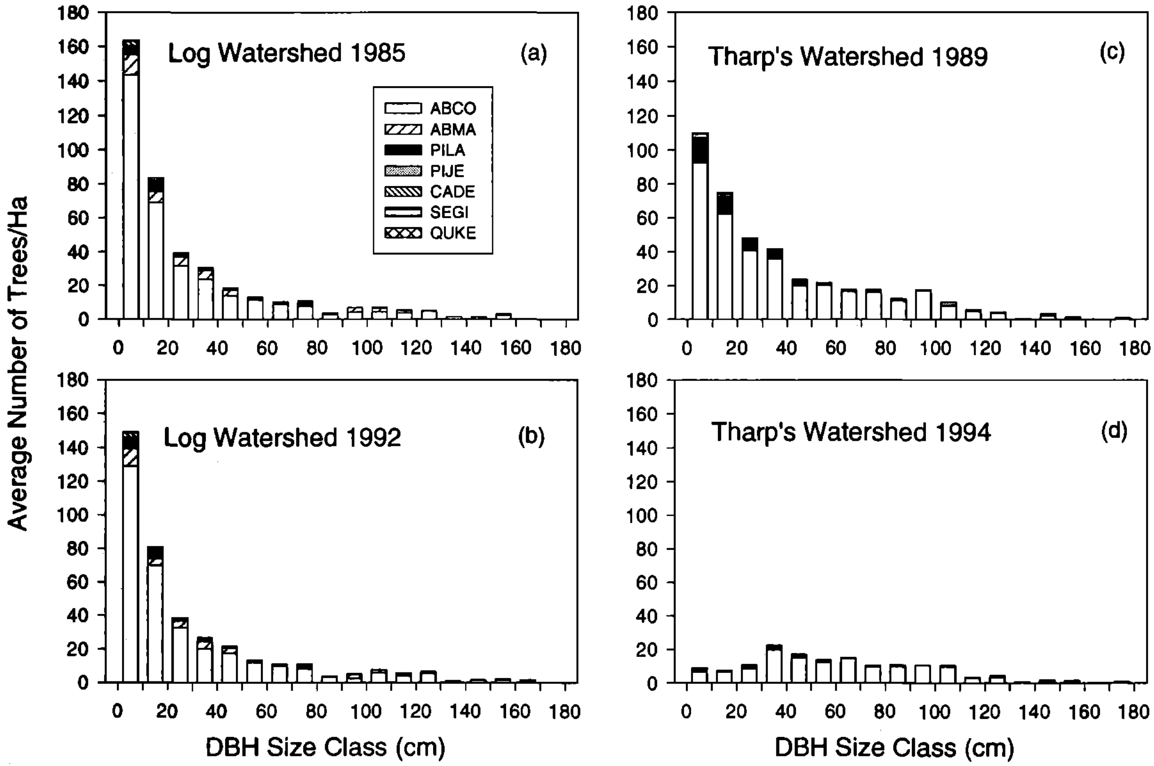

Figure 4. Average size structure of trees ≥1.4 cm tall in 10 cm dbh classes for (a) Log Creek Watershed 1987, (b) Log Creek Watershed 1992, (c) Tharp's Creek Watershed 1989, and (d) Tharp's Creek Watershed 1994 (4 yr post-burn).

conditions over the two time spans were relatively similar. Both *A. concolor* and *P. lambertiana* establishment rates were somewhat higher in the Log Creek watershed, perhaps related to the more mesic conditions and deeper soils than occur on the more south-facing slopes of the Tharp's Creek watershed. The Log Creek watershed also had lower basal area, and presumably canopy cover, than Tharp's in the pre-burn period, resulting in more canopy gaps that would favor ingrowth establishment. *A. magnifica* in the Log Creek watershed had the highest establishment rate of any species in all four stands, and it dominated both in total numbers and mean annual rate of establishment in the Lower Log stand. This is consistent with other studies that have indicated that *A. magnifica* reproduces in greater numbers and on a wider variety of sites than *A. concolor* (Parker 1986, Barbour et al. 1990).

The second 5 yr measurement period for the Tharp's watershed resulted in few ingrowth trees due to the prescribed burn. However, we predict that Tharp's ingrowth numbers will exceed those in the Log Creek watershed in future measurement periods due to the large numbers of seedlings that established in the wake of the 1990 prescribed burn, and the greater numbers and more rapid height growth of these seedlings relative to those in the Log watershed (unpublished data). While a high-light environment can make seedlings more susceptible to drought stress (Kern 1996), fire-created canopy gaps have been hypothesized to increase moisture availability due to the absence of water uptake by mature boundary trees, resulting in rapid growth of plants establishing in these gaps (Demetry 1995). The reduction in litter and duff and the high mortality rates of trees in all canopy classes after the Tharp's burn created conditions of bare mineral soil and increased moisture, light and nutrient availability that favored seedling establishment.

Conclusions

In the absence of fire, annual mortality rates of trees in contemporary Sierra Nevada forests are similar to those in other mixed conifer forests in the west. The higher than expected mortality rates in the *A. magnifica* and *P. lambertiana* populations suggest that these species may be less drought-tolerant and/or more susceptible to disease and insect attack under current forest and climatic conditions than the other species present. In burned stands, tree species died in proportion to their frequency in the watershed. Of the species that sustained mortality as a result of the fire, mortality rates were similar among species, suggesting no one species had an advantage over other species in surviving the fire. There was a stronger relationship between canopy class and mortality rate in burned stands than in unburned stands. In burned stands, subcanopy and intermediate classes had much higher mortality rates than codominant and dominant classes, while in unburned stands, the canopy class with the highest mortality rate varied depending on the stand and time period.

Pathogens and insects are frequently associated with tree death in the Sierra Nevada mixed conifer forests and may play an important role in altering forest structure and composition. Fir canker and dwarf mistletoe were the most important pathogens associated with death in *A. concolor* and *A. magnifica*. White pine blister rust was the most significant pathogen affecting *P. lambertiana*. Fir engravers were associated with approximately a quarter to a third of deaths in *Abies* species. It is very difficult to observe evidence of many pathogens in forest communities (because they may be affecting root systems, heartwood, and foliage high above the ground), therefore we are undoubtedly underestimating their importance in tree mortality as well as their impacts on forest dynamics. While it is often difficult or impossible to determine mortality causes, identifying factors that contribute to mortality and describing how trees die (slow decline or immediate death by physical damage) will help to make forest dynamics models more species-specific in their predictions and will give a more complete picture of the short-term and long-term effects of tree mortality on the forest ecosystem.

In the burned stands, percent volume crown scorch was the predominant factor associated with tree death. For the two species with high enough sample sizes to incorporate into logistic regression models (*A. concolor* and *P. lambertiana*), probability of mortality increased with percentage of crown killed, and for *A. concolor*, decreased with dbh. Models such as these have the potential to improve the ability of managers to predict tree mortality as a result of prescribed burning, and if desirable, to plan burning conditions to meet specific mortality objectives. These models, however, are based on data collected from only one prescribed burn. They should be viewed as preliminary since they have not been tested against independent data and do not incorporate mortality associated with a wide range of fire characteristics that can occur in prescribed burns in different topography, fuel, and weather conditions.

The dramatic declines in basal area (5%–6% per year) and changes in size structure (see Figures 4c and d) in the Tharp's Creek watershed reference stands following the 1990 prescribed burn emphasize the important role of fire in reducing tree densities and thus altering forest structure in Sierran forests. Whereas it is possible that this fire may have burned with higher severity than most past fires in these forests due to high fuel accumulations and ignition techniques, it is also likely that the density of trees was higher than densities were prior to Euro-American settlement. High mortality rates may be a necessary first step toward a more open forest structure. Subsequent burns will be necessary to maintain low fuel loads and reduced tree densities.

The higher rate of ingrowth establishment in the more mesic Log Creek watershed suggests that moisture availability is a main limiting factor to seedling growth and establishment as saplings. While the Tharp's burn killed most of the ingrowth that occurred in the pre-burn period, we expect that the large number of seedlings that established after the burn will result in substantial amounts of ingrowth within the next 10 yr.

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