Tree mortality patterns following prescribed fires in a mixed conifer forest

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Abstract: During the late fall of 2002 we administered three burns in mixed conifer forest sites in the north-central Sierra Nevada. Eight months later we measured fire-induced injury and mortality in 1300 trees. Using logistic regression, an array of crown scorch, stem damage, fuels, and fire-behavior variables were examined for their influence on tree mortality. In Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. & Glend.) Lindl.), and incense cedar (*Calocedrus decurrens* (Torr.) Florin), smaller trees with greater total crown damage had higher mortality rates. Smaller stem diameters and denser canopies predicted mortality best in ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws). Duff consumption and bark char severity increased model discrimination for white fir and incense cedar and California black oak (*Quercus kelloggii* Newberry), respectively. In tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), greater total crown damage in shorter trees resulted in higher mortality rates. Along with tree diameter and consumption of large (>7.6 cm diameter at breast height, DBH) rotten downed woody debris, fire intensity was a significant predictor of overall tree mortality for all species. Mortality patterns for white fir in relation to crown damage were similar among sites, while those for incense cedar were not, which suggests that species in replicated sites responded differently to similar burns. Our results demonstrate actual fire-behavior data incorporated into mortality models, and can be used to design prescribed burns for targeted reduction of tree density in mixed conifer forests.

Résumé : À la fin de l'automne 2002, nous avons réalisé trois brûlages dirigés sur des stations forestières mixtes de conifères dans la région centre-nord de la Sierra Nevada. Huit mois plus tard, nous avons mesuré les blessures et la mortalité induite par le feu sur 1300 arbres. Par le biais d'une régression logistique, nous avons étudié la mortalité des arbres en fonction d'une gamme de variables comprenant le roussissement de la cime, les dommages à la tige, les combustibles et le comportement du feu. Pour le douglas vert (*Pseudotsuga menziesii* (Mirb.) Franco), le sapin argenté (*Abies concolor* (Gord. & Glend.) Lindl.) et le cèdre à rayons (*Calocedrus decurrens* (Torr.) Florin), les plus petits arbres ayant la plus grande quantité de dommages cumulés à la cime étaient associés à une mortalité élevée. La mortalité du pin ponderosa (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws) était fortement associée aux petits diamètres et à des canopées denses. La consommation de litière et la sévérité de la carbonisation de l'écorce ont respectivement augmenté le pouvoir discriminant du modèle pour le sapin argenté, le cèdre à rayons et le chêne noir de Californie (*Quercus kelloggii* Newberry). Dans le cas du chêne à tan (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), les plus forts taux de mortalité ont été observés sur les plus petits arbres ayant la plus grande quantité de dommages cumulés à la cime. Avec le diamètre des arbres et la consommation des gros (>7,6 cm) débris ligneux décomposés au sol, l'intensité du feu était un prédicteur significatif de la mortalité des arbres et ce, pour toutes les espèces. Les patrons de mortalité en fonction des dommages à la cime étaient semblables peu importe la station pour le sapin argenté, mais pas dans le cas du cèdre à rayons, ce qui suggère que les espèces ont réagi différemment à des brûlages similaires selon la station. Nos résultats démontrent que des données réelles de comportement du feu peuvent être introduites dans les modèles de mortalité et peuvent être utilisées pour planifier des brûlages dirigés avec une réduction ciblée de la densité des arbres dans les forêts mixtes de conifères.

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Introduction

Fuel-reduction treatments are one of the highest priorities in the management of western United States forests today. With over 10 million hectares of coniferous forests in moderate or high fire hazard condition classes (National Wildfire Coordinating Group 2001), the National Fire Plan (US Department of Agriculture and US Department of the Interior 2000) and Healthy Forest Restoration Act (United States Congress 2003) have encouraged expedient action to decrease fuel loads in fire-prone coniferous forests (Stephens and Ruth 2005).

Prescribed fire is one of numerous fuel-reduction techniques and has been employed to reduce wildfire severity for

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nearly a century in the northern Sierra Nevada (Biswell 1989). In fire-suppressed, fire-adapted ecosystems, fuel reduction is often an integral component of landscape-level reintegration of historical fire regimes (Covington et al. 1997). Fire's various ecological roles have propelled its application in restoration projects in mixed conifer and ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws) forests of the western USA (Covington et al. 1997; Stephens and Moghaddas 2005*a*). Whether lightning-ignited, experimental, or prescribed, fire can influence soil physical and chemical properties, vegetative species composition and structure, and wildlife habitat (Whelan 1995). Its ultimate role in any ecosystem depends on the frequency, intensity, seasonality, severity, and type of fire, which can be influenced by other disturbance types and climate.

Like other fuel-reduction methods, such as thinning or chipping of understory vegetation and woody material, the application of fire is primarily intended to produce forest stands with specific structures known to mitigate fire severity in the case of an ignition (Brown et al. 2004; Agee and Skinner 2005). Unlike those of other fuel-reduction treatments, the actual effects of prescribed fires on trees are influenced by factors that can extend beyond the manager's control. Fire behavior can vary in relation to fine-scale differences in topography, fuel loads or moisture, or even shifts in relative humidity. Although prescribed burns are administered within a range of acceptable weather and fuel-moisture conditions, the stochastic nature of fire imbues the prediction of its effects with complexity. Often, analyses of postfire tree mortality are based on opportunistic studies lacking pretreatment data or replication (e.g., Peterson and Arbaugh 1986, 1989; Regelbrugge and Conard 1993; McHugh and Kolb 2003), which can result in ambiguity in modeling and statistical analyses (van Mantgem et al. 2001). Agee and Skinner (2005) note that examining the impact of crown fire in dry forests of the western USA is nearly impossible under controlled conditions, even with pretreatment data. Statistically based quantification of the roles played by fire behavior, individual tree species morphology, and fuel distribution and consumption in tree mortality can help managers design prescribed burns for optimal fuel diminution and targeted reduction of tree density.

In contrast to unpredictable wildfire events, prescribed burning provides the opportunity for pre- and post-fire measures of site features and severity as indicated by fuel consumption, as well as direct measures of fire behavior. In the southern Sierra Nevada Mountains of California, duff consumption proved significant in predicting tree mortality following prescribed fire (Stephens and Finney 2002). Litter, duff, and large (>7.6 cm DBH) fuels often comprise the largest single fuel fraction in natural stands (Finney and Martin 1993), and their loads and consumption have been related to root damage and tree injury (Ryan and Frandsen 1991; Swezy and Agee 1991). Consumption of ground fuels is also likely to influence tree mortality, as it indicates the duration of burning and the amount of heat transferred from a fire to tree boles and roots (Ryan 1982).

Direct measures of fire behavior have seldom been used in modeling postfire tree mortality, in large part because of the challenge of quantifying fire characteristics during flame-front passage (van Wangtendonk 1983; Finney and Martin 1993). In-situ measures of flame length can be used to compute fireline intensity (Byram 1959), a unit that describes the rate of heat release over an area of flaming front ($kW{\cdot}m^{-1}$). This aspect of fire behavior is relevant to tree mortality in its direct relationship to the height of convective crown scorch on conifers (van Wagner 1973) and to the presence of any vegetation susceptible to convective heating injury (Finney and Martin 1993). Increases in both flame length and fireline intensity were associated with increased tree mortality in prescribed underburning in the northwestern USA (Reinhardt and Ryan 1988). Flame lengths alone were used to model mortality following a prescribed fire in the understory of a mixed conifer forest in the Sierra Nevada (van Wagtendonk 1983). In a southeastern Canadian boreal forest, authors equilibrated postwildfire bole char height with flame height and then length, concluding that logistic regression models using both tree morphology and fire-behavior indicators outperformed those relying on intrinsic tree sensitivity only (Hely et al. 2003).

Tree features such as radial growth, stem diameter, crown position, or bark thickness have been used to model survival following fire in the western USA for certain conifer species (Ryan and Reinhardt 1988; Mutch and Parsons 1998; Stephens and Finney 2002; van Mantgem et al. 2003). Following a southern Sierra Nevada mixed conifer prescribed burn, the subcanopy or intermediate classes had the highest percent mortality across all species (Mutch and Parsons 1998). The influence of tree stature or intrinsic characteristics on survival is largely reflective of species-specific differences in bark thickness or bark insulative capacity or the presence or absence of adventitious buds. Yet expected patterns are not always exemplified by the data. For example, DBH has not always proved a strong predictor of tree mortality in some mixed conifer stands containing such species as sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine, California black oak (*Quercus kelloggii* Newberry), giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh.), and white fir (*Abies concolor* (Gord. & Glend.) Lindl.) (Swezy and Agee 1991; Mutch and Parsons 1998; Stephens and Finney 2002; van Mantgem et al. 2003). Experimental heat application to small mixed conifer stands yielded no significant difference between bark-related species resistance to cambial damage (van Mantgem and Schwartz 2003). Such discrepancies support the need for highly controlled experiments on tree mortality patterns following fire.

Postfire tree survivorship has been most successfully modeled using measures of foliar damage, such as crown scorch height or percentage of crown volume scorched (Peterson 1985; Ryan and Reinhardt 1988; Peterson and Arbaugh 1989; Stephens and Finney 2002). Some authors have used total crown damage to model mortality, which takes consumption of foliage into account (McHugh and Kolb 2003). These measures quantify the effects of convective heat transfer following flaming or smoldering combustion, and often serve as proxies for fire behavior when direct data are unavailable. The degree of scorch or crown damage a tree can withstand varies with tree size, species, and site-specific factors influencing fire behavior, such as fuel load and burning conditions (Stephens and Finney 2002; McHugh and Kolb 2003). Discrepancies in some tree-injury-based mortality models have led authors to emphasize the importance of site-specific fire behavior and severity information in explaining tree mortality (Ryan and Reinhardt 1988; McHugh and Kolb 2003; van Mantgem and Schwartz 2003). Moreover, a recent review of 21 postfire tree mortality studies in the western USA highlighted the necessity for standardization of site and burn conditions, as well as replication in experimental designs, to increase the quality of tree mortality prediction research (Fowler and Sieg 2004).

In this study the application of prescribed fire for fuel reduction in replicated stands is used to evaluate postfire tree mortality. We explore mortality patterns in three north-central Sierra Nevada mixed conifer forest stands, as part of the National Fire and Fire Surrogate study (McIver and Weatherspoon 2006) in which a series of controlled empirical experiments have been implemented to study the effects of fuel treatments on tree mortality, vegetation structure, fuel loads, and a suite of other ecological variables at 13 locations across the continental USA. Here we test the fuels, inherent tree and tree-injury variables, and fire behavior and severity measures for their capacity to predict postfire survival in 1300 trees. Our objectives are to (*i*) determine which tree-injury and morphological attributes best predict fire-induced mortality in seven mixed conifer forest species, (*ii*) examine the influence of fuel consumption and fire on tree-mortality prediction, and (*iii*) utilize the replicated study design to evaluate variability in tree-mortality patterns among three prescribed burns. To our knowledge this is the first replicated study of the effects of fire on tree-mortality patterns, as well as the first study to incorporate fireline intensity from actual measures of flame height.

Study site

The prescribed burning was conducted in three second-growth mixed conifer forest sites (units 60, 340, and 400) in the north-central Sierra Nevada at the University of California Blodgett Forest Research Station (Blodgett Forest), approximately 20 km east of Georgetown, California. Mixed conifer forests cover approximately 3.2 million ha (7.8%) of California's total land base (California Department of Forestry and Fire Protection 2003). The area of burn units 60, 340, and 400 was 24, 17, and 18 ha, with, on average, 12%, 27%, and 18% slope, respectively.

Blodgett Forest is located at 38°54′45″N, 120°39′27″W, between 1100 and 1410 m above sea level, and encompasses an area of 1780 ha. Soils at Blodgett Forest are well-developed, well-drained Haploxeralfs (Alfisols) derived from either andesitic mudflow or granitic/granodiorite parent materials (Hart et al. 1992). Soils are deep, weathered, sandy loams overlain by an organic forest floor horizon. Common soil depths range from 85 to 115 cm. Tree species growing on this substrate include sugar pine, ponderosa pine, white fir, incense cedar (*Calocedrus decurrens* (Torr.) Florin), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), California black oak, tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), and Pacific dogwood (*Cornus nuttallii* Audubon ex. Torr. & Gray). Because of site-specific edaphic and climatic conditions, conifers at Blodgett Forest (excluding incense cedar) can grow to a height of 27–30 m in 50 years, resulting a Dunning (1942) site I classification.

The climate at Blodgett Forest is Mediterranean with a summer drought period that extends into the fall. Most precipitation, 160 cm on average (Stephens and Collins 2004), falls in winter and spring. Average temperatures in January range between 0 and 8 °C. Summer months are mild, with average August temperatures between 10 and 29 °C, with infrequent summer precipitation from thunderstorms (averaging 4 cm over the summer months from 1960 to 2000) (Stephens and Collins 2004).

Fire was a common ecosystem process in the mixed conifer stands in Blodgett Forest before the policy of fire suppression began early in the 20th century. Between 1750 and 1900, historical fire evaluated at the 3–5 ha spatial scale had a composite fire return interval range of 6–14 years (Stephens and Collins 2004). Forested areas at Blodgett Forest have been repeatedly harvested and subjected to fire suppression for the last 90 years, a management history common to many forests in the Sierra Nevada and Cascade ranges of California (Laudenslayer and Darr 1990; Stephens 2000) and elsewhere in the western USA (Graham et al. 2004).

Materials and methods

Vegetation measurements

Vegetation was measured using twenty 0.04 ha circular plots installed in each of the three treatment units (60 plots in total). Individual plots were placed on a systematic 60 m grid with a random starting point. Plot centers were permanently marked with a pipe, and three witness trees were tagged to facilitate plot relocation after treatments. Tree species, DBH, total height, height to live crown base, plot-level percent canopy cover, and crown position (dominant, codominant, intermediate, suppressed, or understory) were recorded for all trees >10 cm DBH. Similar information was also recorded for all trees >1.37 m tall on a 0.004 ha nested subplot in each of the 20 plots. Canopy cover was measured at 25 points on each 0.04 ha plot using a 5 m by 5 m grid using a GRS densitometer (Geographic Resource Solutions™, Arcata, California) (Gill et al. 2000).

Fuel loads and distribution

Surface and ground fuels were sampled with two random-azimuth transects at each of the 60 plots using the line-intercept method (van Wagner 1968; Brown 1974). A total of 120 fuel transects were installed. One hour time lag (0–0.64 cm) and 10 h time lag (0.64–2.54 cm) fuels were sampled from 0–2 m, 100 h time lag (2.54–7.62 cm) fuels from 0–3 m, and 1000 h time lag (>7.62 cm) and larger fuels from 0–11.3 m on each transect; 1000 h fuels were separated into sound (1000 h (S)) and rotten (1000 h (R)) categories. Duff and litter depths (cm) were measured at 0.3 and 0.9 m on each transect. Fuel depth (cm) was measured at three points along each transect.

Fuel transects were sampled prior to treatment (2001) and 8 months after burning was completed (2003). At the time of fuel remeasurement, windblown scorched needles were on the ground, though their presence did not modify the duff layer from its immediate postburn state. Surface- and ground-fuel loads were calculated using appropriate equations developed for California forests (van Wagtendonk et al. 1996, 1998). Coefficients required to calculate all surface- and ground-fuel loads were arithmetically weighted by the

Table 1. Weather data for prescribed burn treatments during November 2002 in three mixed conifer stands in Blodgett Forest, California.

Variable	Unit 60	Unit 340	Unit 400
Period of active ignition*	1600 on 5 November 2002 to 2400 on 6 November 2002	2300 on 1 November 2002 to 0900 on 3 November 2002	2300 on 3 November 2002 to 1400 on 5 November 2002
Burn period (h)	32	34	39
Backing fire rate of spread ($m \cdot min^{-1}$)	0.3	0.3	0.3
Strip head fire rate of spread ($m \cdot min^{-1}$)	1.5	1.5	1.5
Weather†			
Temperature (°C)‡	10 (7–17)	9 (5–16)	9 (6–17)
Relative humidity (%)‡	29 (19–46)	29 (13–46)	34 (21–41)
Avg. 15-min wind speed ($km \cdot h^{-1}$)‡	1 (1–3)	1.5 (0–3)	1.1 (1–3)
Max. speed of wind gusts ($km \cdot h^{-1}$)	8	8	8
Cloud cover	Clear skies	Clear skies	Clear skies

*Within the time periods shown, active ignitions ceased between 0900 and 1600 daily; on 8 November 2002 rain extinguished all units, with no further burning.
†Data are for entire burn periods.
‡Values are given as the average, with the range in parentheses.

basal area fraction to produce accurate and precise estimates of fuel loads (Stephens 2001).

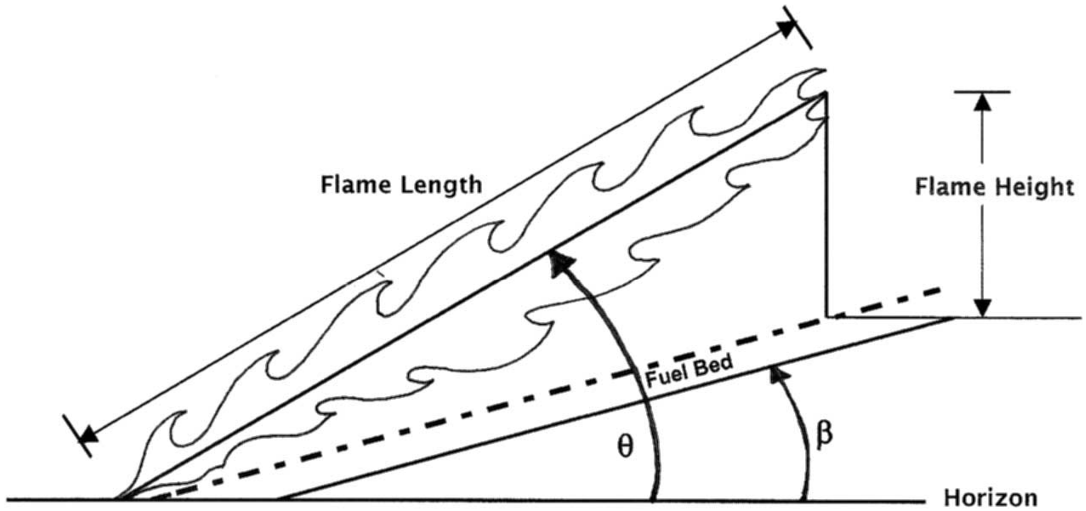
Prescribed fire and resulting tree injury

The three units were burned using strip head fires (Martin and Dell 1978), one of the most common ignition patterns used to burn forests in the western USA. All prescribed burning was conducted during a short period prior to winter precipitation (2–6 November 2002). The last rainfall had occurred in June 2002, meaning that the burns were conducted in what was still considered "fire season". Prescribed-fire prescription parameters for temperature, relative humidity, and wind speed were 0–10 °C, >35%, and 0.0–5 $km \cdot h^{-1}$, respectively; each prescription was met, as shown in Table 1. There were no significant differences between unit weather variables measured every 15 min using on-site HOBO® weather-station data loggers (Table 1). Desired 10 h fuel stick moisture content was 7%–10%. Most active ignitions occurred at night between 1600 and 0900. This was preferred because relative humidity, air temperature, wind speed, and fuel moisture were within predetermined levels that would produce the desired fire effects; fires were "held" during the day, with minimum active ignitions. Ignitions took place on 1 November 2002 in unit 340, 3 November 2002 in unit 400, and 5 November 2002 in unit 60 (Table 1). Temperatures, relative humidity, and wind speeds were similar during ignition and burnout of treated units (Table 1), with residual smoldering being completely extinguished across all units by extensive rainfall beginning on 8 November 2002. The dominant fire behavior was surface fires with occasional torching of trees <25 cm DBH followed by approximately 32–36 h of burnout of duff, stumps, and larger diameter sound woody debris. In contrast to other mixed conifer forest systems, downed woody debris was sparse in these stands (Stephens and Moghaddas 2005*a*), so that any between-stand differences in the longevity of smoldering combustion is not believed to have complicated the interpretation of fire effects.

Scorch heights, percentage of crown volume scorched (PCVS), and initial mortality were assessed 3–5 months after burn completion, between 14 January and 6 March 2003 during periods when foliage was not covered with snow and weather conditions allowed access to research plots. Conifers with no green foliage were considered dead during the postburn scorch remeasurement period and during the summer measurement period in 2003. Trees that were dead during the summer 2003 inventory period were considered dead for this analysis. Other postfire tree-injury measurements, including bark char height and severity, were made in 2003, 8 months after the prescribed burns. Rather than measuring the percentage of crown length scorched, we used visual estimates of PCVS, which has been shown to be a more accurate measure of fire damage (Peterson 1985) and has been successfully used in mortality models (Ryan et al. 1988; Saveland and Neuenschwander 1990; Stephens and Finney 2002). For each tree we recorded PCVS (including buds and foliage killed but not consumed) and the maximum and opposite-maximum crown scorch heights. Total crown damage (TCD) was calculated as PCVS plus the percentage of crown volume consumed (McHugh and Kolb 2003). Crown volume consumption and hence TCD was assumed to be 100% where trees were incinerated, leaving no trace of foliage. For black oak, all foliage-related fire-injury data were omitted, as these deciduous trees had shed their leaves prior to the prescribed burns. Any black oak or tanoak trees with epicormic or adventitious sprouting were considered to be live, regardless of the degree of top kill.

To better isolate stem-related variables for modeling tree mortality (van Mantgem and Schwartz 2003), we used both direct and indirect measures. Stem diameter can be viewed as a proxy for bark thickness and its resulting insulation of the inner cambium against injury (van Mantgem and Schwartz 2003). This indirect measure of tree resistance to fire damage is typically correlated with tree height (Yuancai and Parresol 2001), which may confound its meaning. We therefore also used direct measures of stem damage, including bole char height, percentage of bole circumference charred, percentage of charring below DBH, and bole char severity rating. Bole char severity was rated at maximum char height, below 30.5 cm on the side of maximum char, at the side opposite the maximum char height, and below 30.5 cm on the side opposite maximum charring. Bole char severity was defined as follows: 1 = bark black but not consumed, fissures not blackened; 2 = entire bark and fissures

Fig. 1. Relationships between flame length, slope, and flame height, where β is the slope angle in degrees and θ is the flame tilt in degrees (adapted from Ryan 1981).



blackened but not consumed; or 3 = entire bark and fissures blackened, with significant consumption of bark evident (Ganz et al. 2003). Insects were not detected in the burned units before late May 2003, and no mortality was attributed to insect infestation when inventoried in 2004 (D. Stark, D. Wood, and A. Storer, personal communication, 2005).

Fire behavior

Five passive flame height sensors (Ryan 1981) were positioned in a regular circular pattern in each plot in all three units, totaling 300 sensors. Some sensors fell over during the fire, and after the burn, 86, 91, and 100 sensors were read in units 60, 340, and 400, respectively. The passive flame height sensors were composed of vertically suspended cotton strings. First, the strings were pressure-soaked in a 10% solution of the fire retardant diammonium phosphate $(NH_4)_2PO_4$) in water (Ryan 1981; Finney and Martin 1992). Next, cotter pins were attached at regular intervals to 3 m tall rebar rods, which were then pounded into the soil. Finally, the treated strings were hung so that they passed freely through the cotter pins and were weighted with paper clips to stabilize the string vertically during flame passage (Ryan 1981).

Following the burns, five measurements of the string were documented, including (*i*) the length of the string that was not burned or singed by the fire, (*ii*) the length of completely charred/consumed string, (*iii*) the length at which the string snapped when pulled, or the length of disintegration (Ryan 1981), (*iv*) the length at which the string was completely blackened, and (*v*) the length at which the fine fibers were singed (Finney and Martin 1992).

Ryan (1981) found that the length of string charred to disintegration correlated best with ocular estimates and photographs of continuous flame heights. We used this measure in our calculations of flame length (L, m) from flame-height data from the passive sensors (H, m), using the following equation:

$$[1] \qquad L = \{H[\sin(90 - \beta)]\}/[\sin(\theta - \beta)]$$

where β is the slope angle and θ is the angle of the flame from the horizontal (Fig. 1). Ocular estimates of flame angle during the three burns were compared with photographed flame angles from Finney and Martin (1992) for prescribed fires, and a mean flame angle of 50° was used for the conversion in eq. 1.

Flame lengths are related to fireline intensity (I, $kW \cdot m^{-1}$) in the equation defined by Byram (1959) as

$$[2] \qquad I = 259.83L^{2.17}$$

where L is flame length. This measure describes the rate of heat release per unit length of flaming front ($kW \cdot m^{-1}$) and is associated with fire-caused injuries in aboveground plants (van Wagner 1973). Mean fireline intensity was calculated for each plot within each unit using a plot average of measured flame heights.

Data analysis

The JMP 5.1 Statistical Software package (Sall et al. 2001) and SPSS® Release 14.0 (SPSS Inc. 2005) were employed for our data analyses. Logistic regression procedures have been widely used to model the probability of fire-related tree mortality (Peterson and Ryan 1986; Ryan and Reinhardt 1988; Regelbrugge and Conard 1993; Stephens and Finney 2002; McHugh and Kolb 2003; van Mantgem et al. 2003). This analysis is particularly useful for binary data, such as tree status classified as live or dead following fire, and does not require normally distributed variables. The logistic regression model has the following form:

$$[3] \qquad P_m = 1/\{1 + \exp[-(\beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n)]\}$$

where P_m is the probability of mortality, $X_1 \ldots X_n$ are independent variables, and $\beta_0 \ldots \beta_n$ are coefficients estimated from mortality data.

Before testing variables for predictive capacity in the logistic regression models, we screened both plot-level (canopy cover, fuel loads and distribution, fuel consumption, flame lengths, fireline intensity), morphological (intrinsic tree features such as the height to live crown ratio and DBH), and fire-related tree-injury data for significant pairs (Pearson's product–moment correlation coefficient (r)) >0.50), which precluded their use in a single logistic regression

Table 2. Tree characteristics and fire-caused injuries of live and dead trees of seven species following three prescribed fires in Blodgett Forest.

Species	No. of trees	BA pre/post treatment (%)	TCD (%)	DBH (cm)	$CSR_{opp.}$	$CSR_{max.}$	Tree height (m)	CSR at <30.5 at opp.	CSR at <30.5 at max.	Max. bole char ht. (m)	Percent basal char	Percent char below 1.37 m
White fir (*Abies concolor*)	311 live	26.4 (3.9)	23 (29.9)	30.6 (16.9)	1.7 (1.7)a	1.8 (0.5)a	18.3 (8.8)	1.7 (1.7)	2.4 (0.5)	3.0 (2.2)a	86.4 (22.8)	55.9 (29.0)
	85 dead	27.4 (4.4)	96.6 (16.8)	9.6 (9.3)	2.2 (0.8)a	2.0 (0.5)a	6.3 (5.5)	2.2 (0.8)	2.7 (0.5)	3.0 (1.7)a	97.8 (8.3)	67.0 (25.5)
Incense cedar (*Calocedrus decurrens*)	342 live	22.8 (4.6)	29.5 (33.4)	27.5 (12.8)	2.2 (1.9)	1.7 (0.6)	13.2 (5.8)	2.2 (1.94)	2.5 (0.6)	3.5 (2.3)	91.0 (19.5)	67.3 (28.0)
	86 dead	22.0 (5.0)	92.8 (20.8)	13.8 (8.6)	2.7 (0.5)	2.0 (0.6)	6.5 (3.3)	2.7 (0.4)	2.9 (0.5)	4.0 (2.1)	99.6 (3.0)	83.5 (18.7)
Tanoak (*Lithocarpus densiflorus*)	74 live	5.1 (5.0)	21.9 (30.9)	25.8 (11.0)	1.1 (1.1)	1.5 (0.6)a	14.8 (6.2)	1.1 (1.1)	1.9 (0.7)	0.9 (0.9)a	63.1 (36.0)	26.1 (23.8)
	44 dead	3.8 (3.8)	92.3 (24.2)	10.6 (15.4)	1.8 (1.0)	1.9 (0.5)a	5.6 (4.8)	1.8 (1.0)	2.8 (0.4)	1.6 (2.6)a	92.1 (22.3)	36.9 (23.7)
Sugar pine (*Pinus lambertiana*)	34 live	10.1 (2.0)	15.1 (25.4)	62.4 (27.0)	1.6 (0.9)a	1.5 (0.5)a	29.9 (10.9)	1.6 (0.9)a	2.0 (0.5)a	4.0 (3.1)a	87.8 (21.2)a	48.1 (30.6)a
	2 dead	10.5 (2.0)	97.5 (3.5)	15.1 (1.3)	2.5 (0.7)a	2.0 (0)a	10.6 (3.6)	2.5 (0.7)a	2.5 (0.7)a	4.5 (3.5)a	100a	77.5 (31.9)a
Ponderosa pine (*Pinus ponderosa*)	51 live	10.3 (4.2)	10.7 (18.0)	47.2 (29.0)	1.7 (0.9)a	1.4 (0.5)a	25.3 (14.0)	1.7 (0.9)a	2.1 (0.5)a	3.8 (2.4)a	92.8 (15.3)a	58.7 (31.4)a
	10 dead	10.9 (4.5)	100 (0)	2.5 (4.7)	2.5 (0.7)a	2.0 (1.4)a	2.9 (3.6)	2.5 (0.7)a	2.5 (0.7)a	1.0 (0)a	100a	35.0 (14.1)a
Douglas-fir (*Pseudotsuga menziesii*)	135 live	19.7 (4.7)	0.4 (4.8)	42.2 (20.6)	1.7 (1.0)	1.8 (0.4)a	23.4 (9.5)	1.7 (1.0)	2.2 (0.6)	3.6 (2.2)	87.9 (22.6)	59.2 (30.9)
	28 dead	21.0 (5.1)	39.2 (49.6)	12.7 (6.3)	2.4 (0.5)	2.0 (0.2)a	8.5 (4.1)	2.4 (0.5)	2.5 (0.6)	2.5 (1.5)	100 (0)	72.4 (27.8)
California black oak (*Quercus kelloggii*)	40 live	5.7 (3.0)	na	26.1 (28.8)	1.2 (1.0)	1.5 (0.7)a	11.4 (10.7)	1.2 (1.1)	2.2 (0.7)a	1.4 (1.3)a	79.2 (25.8)	29.8 (25.8)
	54 dead	4.3 (2.2)	na	7.6 (16.2)	2.5 (0.7)	1.9 (0.7)a	4.4 (6.2)	2.5 (0.7)	2.6 (0.5)a	1.7 (1.6)a	100 (0)	52.0 (25.0)

Note: Values are given as the mean with the standard error in parentheses. Within a species, values followed by the same letter in a column are not significantly different ($p < 0.05$) in the Wilcoxon/Kruskal–Wallis rank sum test for nonparametric data. All other pairs are significantly different. BA is percent composition by basal area; TCD is total crown damage (scorch + consumption); DBH is the diameter at breast (1.37 m) height; $CSR_{opp.}$ is the bole char severity rating at the side opposite where maximum bole char occurred; $CSR_{max.}$ is the bole char severity rating at the highest bole scorch position; CSR at <30.5 at opp. is the bole char severity rating at heights <30.5 cm from the ground on the side opposite maximum bole scorch; CSR at <30.5 at max. is the bole char severity rating at heights <30.5 cm from the ground on the side where maximum height of bole scorch occurred; percent basal char is the percentage of bole circumference charred; percent char below 1.37 m is the percentage of charring below this height on the tree bole; max. bole char ht. is the maximum height of a char on the tree bole.

model. All independent morphological and tree-injury variables were tested for significant differences (Wilcoxon/ Kruskal–Wallis rank sum test, $p < 0.05$) between live and dead trees within each species (Table 2).

Independent variables that were not significantly correlated were used for the logistic regression models. The initial reverse-stepwise multiple logistic regression approach was used to explore all the variables for possible predictive capacity. After the most influential predictors were identified, model coefficients were estimated using a maximum likelihood fitting procedure (Bishop et al. 1975), and final models only included significant covariates according to the generalized Wald statistic and the likelihood ratio test ($p < 0.05$). Six outliers out of the 1300 trees measured were identified using analysis of residuals in the various logistic regression models. Data for these trees were far outside the range of the other 1294, and as they were likely the result of field sampling errors, they were removed from the analysis.

Relative goodness of fit, or deviance (G^2), was assessed using a likelihood ratio test to compare the fitted model with one using only constants. Hosmer and Lemeshow's goodness-of-fit test (Hosmer and Lemeshow 2000) was used to determine whether the model-predicted mortality values differed from observed mortality values, with p values >0.05 indicating no difference. Classification accuracy based on this test was calculated. We also employed the "lack-of-fit" test (JMP 5.1; Sall et al. 2001), which uses the pure-error negative log-likelihood for every possible combination (i.e., polynomials, crossed terms) of the regressor values in a model to test whether any additional, more complex terms need to be added.

Model discrimination was evaluated using receiver operating characteristic (ROC) curve analysis (Saveland and Neuenschwander 1990). This curve is generated by plotting the frequency of correct predictions or hits (i.e., trees predicted and observed to be live) versus the frequency of false alarms (i.e., trees predicted to be live but observed to be dead) as the decision criterion varies from 0 to 1 (Egan 1975). This procedure has been used to assess the accuracy of the logistic regression model in other fire-mortality studies (Ryan and Reinhardt 1988; Finney and Martin 1993; Regelbrugge and Conard 1993; Stephens and Finney 2002; McHugh and Kolb 2003; van Mantgem et al. 2003). The area under the ROC curve corresponds to the concordance of a correct prediction and classification of observations. A maximum value of 1.0 signifies no error in model prediction, while a value of 0.5 signifies the model's inability to make predictions that are better than chance occurrence (Saveland and Neuenschwander 1990). ROC values higher than 0.70 are generally considered indicative of good model discrimination (Hosmer and Lemeshow 2000). Values higher than 0.90 indicate very high discrimination accuracy in the logistic regression model.

Logistic regression analyses were preformed for each of the seven tree species, except dogwood for which there were too few individuals. For tanoak, sugar pine, ponderosa pine, Douglas-fir, and black oak, data were aggregated for the three units, owing to insufficient trees in some units. Mortality patterns in white fir and incense cedar were analyzed for each unit individually, as well as for all units merged. To compare the separate unit models with the model for all units merged, we used the deviance, G^2. The difference between the sum of G^2 values for individual unit models and the G^2 value for the merged-units model is asymptotically distributed as χ^2, and its significance can be tested on that basis to ascertain the similarity of the tree-mortality response to a given variable among the units (Freedman 2005). To examine patterns and influences of fire behavior, and to determine entrance into regression equations (Wyant et al. 1986), we used two one-way ANOVAs on fire intensity between species and between live and dead trees for each unit. To perform multiple comparisons between fire intensity in relation to species composition and mortality, we used Tukey's honestly significant difference (HSD) test (Zar 1999). Mortality models incorporating fireline intensity used plot-level mean intensity values. These mean plot values were applied to all trees within the corresponding 0.04 ha plots.

Results

Species' characteristics and mortality rates

Mean preburn stand values, including species composition and percent basal area, percent canopy cover, average quadratic mean DBH, tree density, and tree heights, were similar for the three units (data not shown; see Stephens and Moghaddas 2005*b*). Percent composition by basal area for each species did not change significantly following the prescribed fire (Table 2). Of the independent variables used in the mortality models, TCD, DBH, and tree height values differed between live and dead trees of every species (Table 2). Live trees had larger diameters and were taller than most dead trees. Bole char severity ratings at either maximum char height or opposite this height were similar in live and dead trees for all species except incense cedar (Table 2). Bole char severity was relatively greater at the base of the tree opposite the maximum char height than at the highest bole scorch location (Table 2). Excluding Douglas-fir and black oak, dead trees sustained over 90% TCD, on average.

Overall mortality was 30% in unit 60, 17% in unit 340, and 26% in unit 400. Mortality ranged between 3.2% and 58% for individual tree species 8 months after the prescribed burn (Table 3). Sugar pine had the lowest overall mortality rate, but was also the least represented in the units, with only 2 dead of the total of 36 individuals (Table 3). Only one (dead) tanoak >75 cm DBH was observed in the units, explaining the high percent mortality for that DBH class. For all species other than black oak, mortality tended to decrease with increasing DBH (Table 3). The highest overall mortality rate was observed in tanoak and black oak, even though top-killed but sprouting individuals were not included in the tally of dead trees.

Fire severity and intensity and influence of tree species

With few exceptions, ground (duff and litter) and surface fuel loads and percent consumption in the three units were similar (Table 4). Unit 400 differed from unit 60 in 100 h fuel load and consumption of 1000 h fuels, while unit 340 had lower 1000 h (S) fuel consumption (Table 4). The post-treatment inventory of woody debris included existing 1000 h fuels that had not been completely consumed during the prescribed burn, as well as new coarse woody debris created by the downing of snags by the prescribed burn. Some

Table 3. Postfire percent mortality rates for seven mixed conifer species belonging to different DBH classes in Blodgett Forest stands.

Species	DBH (cm) 2.5–25	25–51	51–76	>76	All
White fir (*A. concolor*)	25.99 (16.95)	1.88a (1.79)	1.33 (2.30)	0.00	16.83a (12.21)
Incense cedar ©. *decurrens*)	27.11 (10.29)	2.11a (2.36)	6.67 (11.55)	na	17.72a (9.92)
Tanoak (*L. densiflorus*)	38.03 (32.94)	0.00a	na	100a	58.01b (36.36)
Sugar pine (*Picea lambertiana*)	28.57 (0)	0.00a	0.00	0.00	3.17a (5.50)
Ponderosa pine (*P. ponderosa*)	33.34 (38.19)	0.00a	0.00	0.00	12.17a (12.0)
Douglas-fir (*Pseudotsuga menziesii*)	37.40 (23.46)	2.78a (4.81)	0.00	0.00	26.44 (10.11)
Black oak (*Q. kelloggii*)	60.77 (14.31)	22.92b (14.73)	10.0 (14.14)	25.0b (35.36)	52.55b (24.89)

Note: Values are given as the mean with the standard error in parentheses. Values followed by different letters in the same column are significantly different (Tukey's HSD test, $\alpha = 0.05$).

Table 4. Fuel characteristics for three mixed conifer stands in Blodgett Forest subjected to prescribed burning.

Fuel type	Unit 60	Unit 340	Unit 400
Preburn time lag fuel class load (Mg/ha)			
Total	129.20 (52.41)	114.71 (74.50)	125.33 (97.53)
1 h	1.25 (0.87)	1.13 (1.04)	0.9 (0.71)
10 h	4.53 (3.23)	5.53 (4.97)a	2.9 (2.3)b
100 h	9.93 (8.18)a	6.17 (7.15)b	4.25 (4.12)b
1000 h sound	7.52 (16.82)	7.91 (17.04)	2.57 (5.36)
1000 h rotten	14.18 (23.31)	29.02 (40.86)	26.62 (65.62)
Preburn ground fuel depth (cm)			
Duff	3.38 (2.83)	2.5 (1.34)	4.0 (3.79)
Litter	2.79 (1.69)	2.05 (1.98)	2.14 (1.60)
Postburn fuel consumption (%)			
Total	71.95 (27.66)	60.17 (48.17)	65.10 (40.11)
1 h	47.70 (44.63)	46.01 (42.73)	38.02 (39.82)
10 h	41.54 (70.44)	53.36 (81.30)	40.21 (85.29)
100 h	44.56 (70.63)	46.78 (60.72)	63.84 (58.15)
1000 h sound	53.58 (51.62)	17.71 (142.80)	45.81 (118.66)
1000 h rotten	70.68 (51.28)a	91.31 (23.45)ab	97.88 (10.62)b
Duff	84.98 (34.10)	78.88 (49.52)	90.67 (19.61)
Litter	68.84 (38.43)	69.20 (43.36)	52.26 (54.90)

Note: Values are given as the mean with the standard error in parentheses. Values in the same row followed by different letters are significantly different ($p < 0.05$) in the Wilcoxon/Kruskal–Wallis rank sum test for nonparametric data.

snags smoldered at the base for several days before falling or, because of their weakened state, were blown over by winter storms. These new pieces may account for differences in 1000 h (S) fuel consumption in unit 340. Overall fuel consumption was greater than 60% for all stands, with the highest levels in the 1000 h (R) fuel classes (Table 4).

Fireline intensity did not differ significantly among units: 235.23 ± 37.32, 295.10 ± 23.97, and 285.79 ± 21.13 $kW{\cdot}min^{-1}$ (mean ± standard error) in units 60, 340, and 400, respectively. Both species composition and tree status influenced fireline intensity in units 60 and 340 and for all units merged, but not in unit 400 (Table 5). Fireline intensities were significantly higher in plots with more dead trees for all units except 400, and were higher in plots with incense cedar than in those with Douglas-fir in unit 340. Also in unit 340, fire intensity was greater in plots with more incense cedar than in those with more tanoak or white fir (Table 5). Preburn 1000 h (S) fuel load was higher in the unit 340 plots with incense cedar than in those with white fir and tanoak, and fuel depths were greater than for plots with more white fir (data not shown).

Mortality modeling using logistic regression

Our logistic regression analysis was performed in three parts. First, we analyzed species-specific mortality predictors to produce optimal models for each species in the combined units. Next, we performed logistic regression on the two most populous species, white fir and incense cedar, in each of the three individual units and then in the combined units to address variability between the replicated sites. Finally, we evaluated the best models for each unit using fireline intensity as a requisite parameter.

Significant models were produced for all but one species. With only two dead individuals, a significant maximum like-

Table 5. ANOVA for fireline intensity along with multiple comparisons of species and tree-status effects on fireline intensity in the three mixed conifer forest units.

		Fire intensity*											
		ANOVA			Tree status		Species						
Unit	Source	*n*	*F*	*p*	Live	Dead	Black oak	Douglas-fir	Incense cedar	Ponderosa pine	Sugar pine	Tanoak	White fir
60	Species	151	2.32	0.0359			121.84 (67.34)	261.75 (84.42)	204.66 (50.58)	82.21 (76.61)	314.45 (182.36)	77.10 (315.86)	341.37 (42.59)
	Live or dead	151	5.80	0.0173	193.20 (31.29)a	328.24 (46.54)b							
340	Species	366	3.64	0.0008			118.63 (114.97)	155.92 (88.51)a	482.11 (265.52)b	538.43 (229.95)	190.36 (153.30)	257.69 (45.99)ac	246.20 (40.81)ac
	Live or dead	366	28.22	0.0001	239.75 (25.95)a	583.14 (59.20)b							
400	Species	432	1.35	0.2436			87.944 (202.88)	403.97 (54.55)	308.47 (38.45)	152.88 (101.44)	328.62 (108.44)	na	293.64 (43.42)
	Live or dead	432	0.42	0.5166	302.11 (28.10)a	337.13 (46.07)a							
All units	Species	949	2.2638	0.0274			116.05 (68.83)	320.96 (40.2)	311.32 (25.73)	156.96 (67.32)	289.63 (79.48)	255.91 (45.43)	279.21 (25.64)
	Live or dead	949	17.803	0.0001	248.17 (16.49)a	393.29 (30.18)b							

*Values are given as the mean with the standard error in parentheses. Values in the same row followed by different letters differ significantly between live and dead trees according to the Wilcoxon/Kruskal–Wallis rank sum test. Significant differences between values for each species are denoted by different letters following values in the same row for each unit (Tukey's HSD test, $\alpha = 0.05$). Values did not differ overall between units (Tukey's HSD test, $\alpha = 0.05$).

Table 6. Logistic regression mortality coefficients for best overall models using morphological and tree-injury measures for each species, including the receiver operating characteristic (ROC) curve value and the likelihood ratio χ^2 statistic (G^2) with corresponding statistical significance ($\alpha = 0.05$).

Species in all units	β_0	β_1	X_1	β_2	X_2	β_3	X_3	ROC	G^2	p (≤)
White fir (*A. concolor*)	−47.8470 (11.6970)	−0.1210 (0.0400)	DBH	0.5030 (0.1180)	TCD	0.0360 (0.0140)	Duff	0.998	371.3	0.0001
Incense cedar *C. decurrens*)	−3.9574 (1.1049)	−0.1892 (0.0416)	DBH	0.0540 (0.0086)	TCD	1.2266 (0.3593)	$CSR_{max.}$	0.95	198.79	0.0001
Tanoak (*L. densiflorus*)	−2.0216 (1.1436)	−0.1144 (0.0627)	Tree height*	0.0431 (0.00992)	TCD	na	na	0.947	86.76	0.0001
Ponderosapine (*P. ponderosa*)	−4.1607 (2.1657)	−0.2542 (0.1129)	DBH	0.0922 (0.0452)	Canopy cover	na	na	0.958	31.64	0.0001
Douglas-fir (*Pseudotsuga menziesii*)	4.2076 (1.4244)	−0.2979 (0.0829)	DBH	0.0359 (0.0183)	TCD	na	na	0.957	88.67	0.0001
Black oak (*Q. kellogii*)	−5.6977 (2.2511)	2.2393 (0.9352)	$CSR_{opp.} < 30.5$	na	na	na	na	0.861	12.64	0.0004

Note: All regression coefficients differ significantly from zero at $p \le 0.05$, except tree height at $p \le 0.10$; β_0 is the intercept; β_n are model coefficients; X_n are model parameters; "canopy cover" is percent canopy closure; "duff" is percent consumption of duff layer.

lihood estimate could not be obtained for sugar pine. According to generalized Wald and likelihood ratio statistics, TCD was a consistently stronger variable in predicting mortality than either PCVS or percentage of crown volume consumed, and as these measures are correlated, we used only the strongest parameter in models where each was significant (McHugh and Kolb 2003). Optimal models for each species based on G^2, ROC, and the lack-of-fit test are shown in Table 6. Only tree and stand features yielded a significant model for ponderosa pine mortality, with predicted mortality increasing in plots where diameters were smaller and canopy cover was more closed (Fig. 2). DBH was a significant independent variable in all species but tanoak, where the univariate model based on TCD could only be improved by the addition of tree height measurements (Table 6, Fig. 3). Predicted tree mortality increased with increasing TCD and decreasing DBH in white fir (Fig. 4), Douglas-fir (Fig. 5), and incense cedar (Fig. 6).

The addition of duff consumption and bole char severity rating at the highest scorch location to the bivariate models based on DBH and TCD for white fir and incense cedar, respectively, reduced lack of fit and increased model accuracy (ROC) (Table 6). All models were highly significant according to the likelihood ratio statistic (G^2), and ROC values indicated very good overall model accuracy, while the lack-of-fit test showed that models could not be improved with the addition of more complex regressor terms ($p > 0.05$). For all species other than tanoak, the models were better at predicting survivorship than mortality, notably in ponderosa pine and black oak (Table 7). Overall (net) classification correctness was high. H-L statistics were >0.05 for all models, demonstrating insignificant differences between predicted and observed tree status (Table 7).

Using replicated sites and fires for mortality analysis of two conifer species

Only incense cedar and white fir were populous enough to support a logistic regression analysis for each of the three units separately. For each unit and the two species, optimal models were univariate, based on TCD alone (data not shown). Each model produced a significant maximum likelihood estimate and demonstrated very high discrimination accuracy, with ROC values ranging from 0.90 to 0.99. To assess the variability in the models between units, we also performed the regression analysis on each species for all three units merged, limiting the model again to the same and strongest univariate predictor, TCD. We took the measure of deviance, G^2, in the logistic regression analysis and compared it with the sum of G^2 values for each separate unit (e.g., for incense cedar, $G^2 = 233.27$ for the sum of units and $G^2 = 204.45$ for the smaller model; for white fir, $G^2 = 259.63$ for the sum of units and $G^2 = 263.83$ for the smaller model). The difference was significant for incense cedar but not for white fir ($\alpha = 0.05$), implying that the sites were actual replicates of the response to fire-induced crown damage for white fir but not incense cedar.

Fireline intensity as a requisite variable in mortality prediction

It is not surprising that although the ANOVA reported overall differences between mean fireline intensities for the

Fig. 2. Estimated mortality rates for ponderosa pine in relation to diameter at breast height (DBH) predicted by prefire canopy cover following prescribed fire in three mixed conifer stands in Blodgett Forest, California. As actual canopy cover ranged from 60% to 71%, all other associated mortality values are extrapolated.

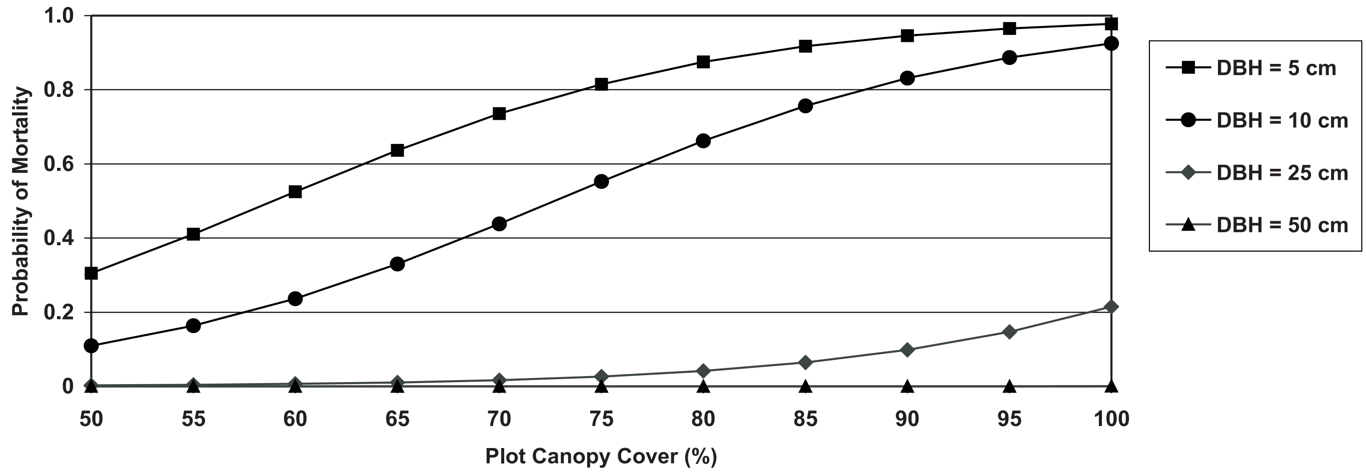


Fig. 3. Estimated mortality rates for tanoak resulting from total crown damage (TCD) following prescribed fire in the three mixed conifer stands.

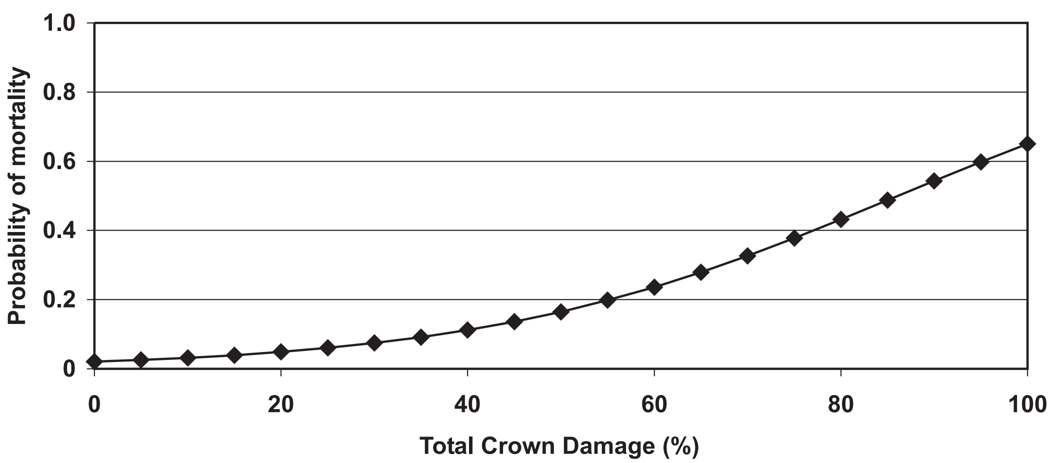


Fig. 4. Estimated mortality rates for white fir in different DBH classes resulting from TCD following prescribed fire in the three mixed conifer stands.

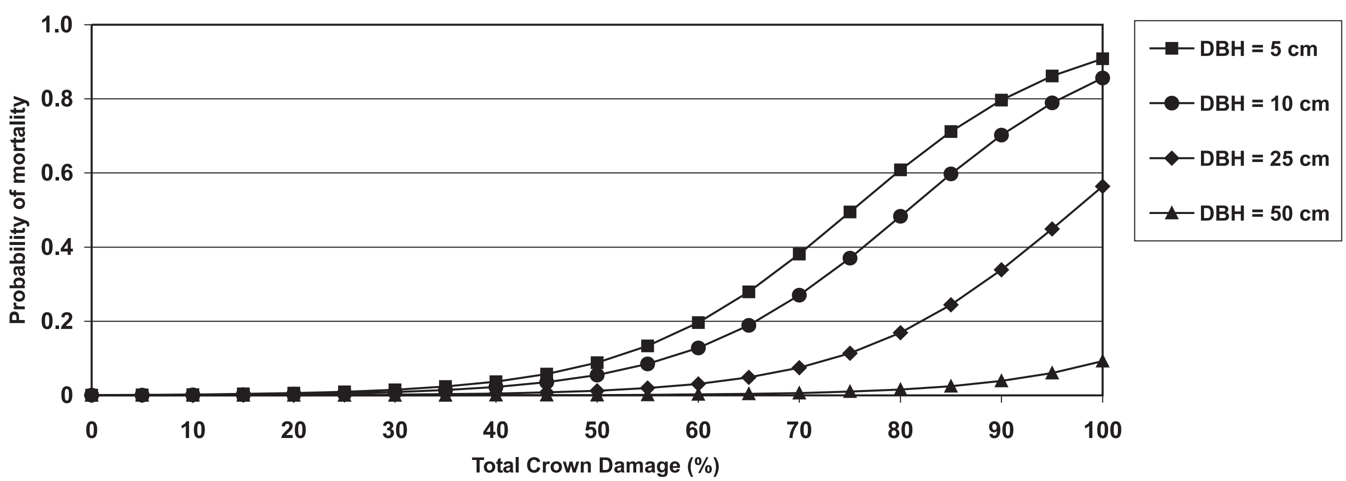


Fig. 5. Estimated mortality rates for Douglas-fir in different DBH classes resulting from TCD following prescribed fire in the three mixed conifer stands.

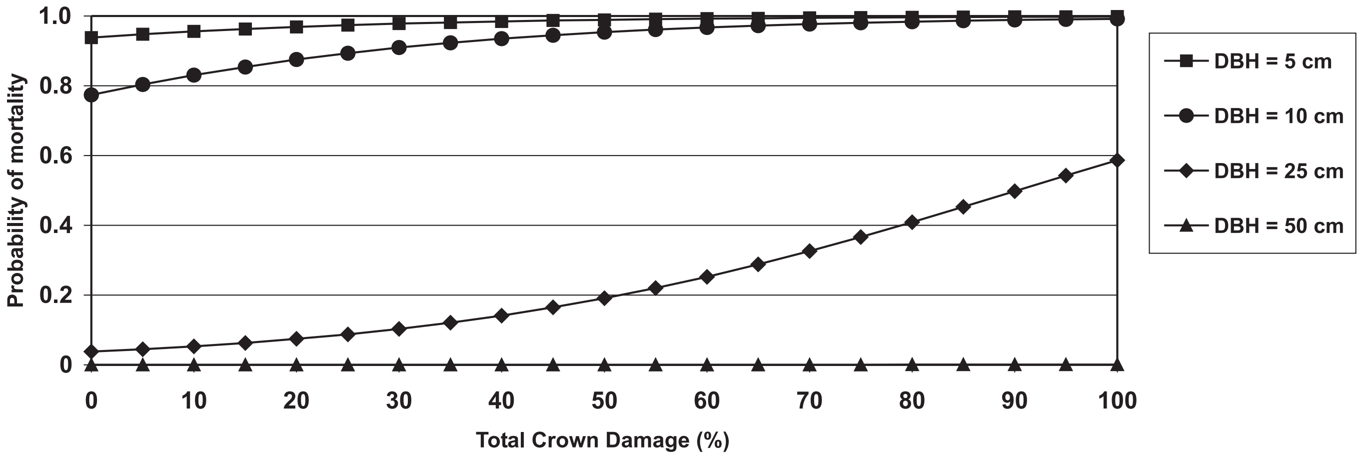
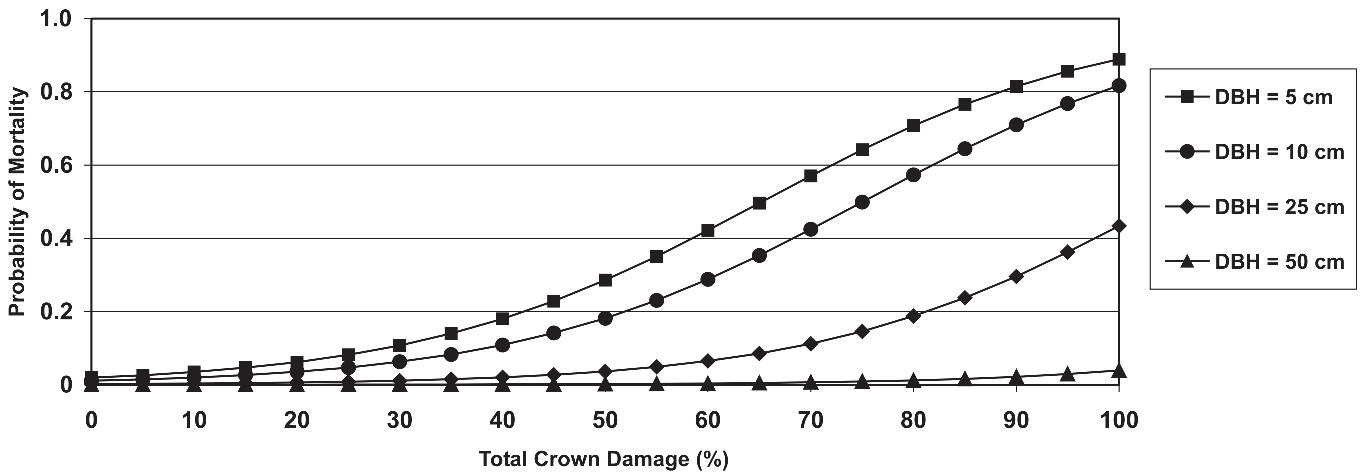


Fig. 6. Estimated mortality rates for incense cedar in different DBH classes resulting from TCD following prescribed fire in three stands.



combined units and the different species in unit 60, Tukey's test did not. In contrast to Student's *t* test, Tukey's test is considered conservative in its ability to detect differences in groups of data (Zar 1999, p. 214). Because our ANOVA showed the mean fireline intensity values for species in each unit to be similar, we did not perform a species-specific logistic regression using intensity. Instead we performed our regression modeling on all species within each unit and on the combined data set.

In concert with measures of tree morphology, fireline intensity proved to have a significant effect on predicted mortality when all trees were combined (Table 8), but generally produced models with lower ROC and G^2 values than the optimal-fit models for each species. Overall predicted tree mortality increased with higher fireline intensity and smaller tree diameters in units 340 and 400 (Table 8). In unit 60, tree height was the only variable with a significant effect on tree-mortality prediction when intensity was incorporated into the model (Table 8). The addition of a fire-severity variable, the consumption of 1000 h (R)) fuels, improved the models in unit 400 and for all units combined. The relationships between mortality and intensity were similar between the units. ROC values for the models using fireline intensity indicated very good model discrimination, and the H-L statistic was insignificant (Table 7).

Discussion

Our results confirm those from previous studies in demonstrating how both crown damage and tree diameter are important indicators of coniferous species survival following fire (Peterson and Arbaugh 1986; Ryan and Reinhardt 1988; Saveland and Neuenschwander 1990; Regelbrugge and Conard 1993; Stephens and Finney 2002; McHugh and Kolb 2003). A tree's ability to survive fire is explained in part by its bark's ability to protect it against vascular cambial damage (Peterson and Arbaugh 1986; Ryan et al. 1988; van Mantgem and Schwartz 2003; Bova and Dickinson 2005). The linear relationships between bark thickness and diameter for various species are well documented and have been used as predictors in other works (Ryan and Reinhardt 1988; van Mantgem and Schwartz 2003). The significance of diameter in all of our conifer mortality models is seen in other studies of some of these species (Wyant et al. 1986; Regelbrugge and Conard 1993; Mutch and Parsons 1998; Stephens and Finney 2002).

Table 7. Evaluation of correct predictions and goodness of fit for logisitic models depicting tree mortality following three prescribed burns at Blodgett Forest.

Species and units modeled	Independent variables	C_dO_d	C_LO_L	Overall	R^2	H-L statistic
White fir (*A. concolor*) (all)	DBH, TCD, duff	97.6	99	98.7	0.947	0.618
Incense cedar *C. decurrens*) (all)	DBH, TCD, $CSR_{max.}$	71	94.1	90.1	0.647	0.125
Tanoak (*L. densiflorus*) (all)	Tree height, TCD	88.9	87.8	88.2	0.705	0.253
Ponderosa pine (*P. ponderosa*) (all)	DBH, canopy cover	60	98	91.8	0.685	0.999
Douglas-fir (*Pseudotsuga menziesii*) (all)	DBH, TCD	67.9	97	92	0.701	0.978
Black oak (*Q. kellogii*) (all)	$CSR_{opp.}$	60	90.9	81.3	0.413	0.392
All (unit 60)	*I*, tree height	75.6	87.5	83.9	0.595	0.406
All (unit 340)	*I*, DBH	71.4	97.4	93.4	0.655	0.312
All (unit 400)	*I*, DBH, con.1000R	65.5	92.9	85.9	0.586	0.352
All (all units)	*I*, DBH, con.1000R	67.9	94	88.1	0.602	0.545

Note: Trees with predicted mortality ≥0.5 were classified as dead (C_d), while trees with predicted mortality <0.5 were classified as live (C_L). C_dO_d is classified dead, observed dead; C_LO_L is classified live, observed live; R^2 is Nagelkerke's pseudo-R^2 for logistic regression; H-L is the Hosmer–Lemeshow goodness-of-fit statistic; *I* is fireline intensity (kW·m^{-1}); and con. 1000R is consumption of 1000 h time lag fuels. For an explanation of other abbreviations see Table 2.

Table 8. Logistic regression mortality coefficients for best models using fireline intensity (*I*), with ROC curve values, and the likelihood ratio χ^2 statistic (G^2) with corresponding statistical significance (α = 0.05).

	β_0	β_1	X_1	β_2	X_2	β_3	X_3	ROC	G^2	p (≤)
Unit 60	1.0535 (0.3900)	0.0017 (0.0008)	*I*	–0.2390 (0.0444)	Tree height	na	na	0.9144	81.23	0.0001
Unit 340	1.5021 (0.4800)	0.0024 (0.0004)	*I*	–0.2505 (0.0344)	DBH	na	na	0.9418	172.02	0.0001
Unit 400	1.5381 (0.4924)	0.0013 (0.0003)	*I*	–0.2476 (0.0284)	DBH	0.0207 (0.0045)	Con. 1000R	0.912	237.49	0.0001
All units	1.0337 (0.2497)	0.0015 (0.0002)	*I*	–0.2210 (0.0171)	DBH	0.0219 (0.0031)	Con. 1000R	0.9223	492.98	0.0001

Note: Regression mortality coefficients are given as the mean with the standard error in parentheses; all differ significantly from zero at p ≤ 0.05. β_0 is the intercept; β_n denotes the model coefficient; X_n denotes the model parameter; *I* is fireline intensity (kW·m^{-1}); DBH is diameter at breast height (cm); and con. 1000R is consumption of 1000 h time lag fuels that were partially decomposed prior to the burn.

Mortality trends in six tree species

The strongest set of predictors of white fir mortality, DBH, TCD, and duff consumption, were nearly identical with those reported by Stephens and Finney (2002): DBH, duff consumption, and PCVS. Duff consumption has not, to our knowledge, been used to model white fir mortality in other reports. This may be due to the lack of information on pretreatment fuel load in studies of white fir mortality, or stronger alternative predictor variables, although the reasons are not always clear (Mutch and Parsons 1998; van Mantgem et al. 2003). Where prefire data were not available, other studies used ground char severity measures (Ryan and Noste 1985) to qualify damage to fine roots in other conifer species, concluding that severity was greater near dead trees (Peterson 1984; Swezy and Agee 1991; McHugh and Kolb 2003). The significance of the duff-consumption parameter may reflect longer flame-residence times. Prolonged combustion of the forest floor can kill fine roots as well as damage white fir cambium, which is protected by a thinner bark layer than its mixed conifer counterparts (van Mantgem and Schwartz 2003). Van Mantgem et al. (2003) found white fir growth rates inversely proportional to mortality rates, and although we did not measure growth specifically, extrapolation of rates indicates that the high proportion of suppressed white fir trees with smaller diameters also had lower growth rates than their upper-canopy neighbors.

The probability of white fir survivorship for different DBH classes subjected to crown fire damage contrasted sharply between previous studies in mixed conifer stands (Mutch and Parsons 1998; Stephens and Finney 2002). Our results more closely resemble those developed by Stephens and Finney (2002), where predicted white fir mortality ranges between 20% and 40% for trees in the 10 cm DBH class with 60% crown damage. For larger size classes (>25 cm DBH) our model predicts lower mortality rates for white fir and ponderosa pine than those reported by Stephens and Finney (2002). In contrast to the old-growth characteristics of the southern Sierra Nevada stands where Stephens and Finney (2002) conducted their research, our forests were younger (~90 years old) and therefore likely more vigorous, which would result in lower mortality rates given the same degree of fire-induced injury.

The low number of dead trees (10 of 61 in total) was likely the cause of the 40% classification error for dead ponderosa pines. We observed no mortality in ponderosa pines measuring >25 cm DBH, limiting our model's capacity to detect differences in survivorship between the larger DBH classes. Still, DBH was a strong indicator overall for ponderosa pine mortality (Wyant et al. 1986; Regelbrugge and Conard 1993; Stephens and Finney 2002). That TCD was not significant in predicting this species' survivorship may be a function of its height and stature in the forest profile (Mutch and Parsons 1998). Pines were the tallest species in our sites and most were in the dominant or codominant canopy stratum. Those that died as a result of crown damage and consumption were completely scorched, suppressed trees, which made regression modeling of mortality in relation to TCD largely inapplicable. Instead, local plot canopy cover proved to be a strong predictor. We are unaware of any other study that has investigated how preburn canopy cover could affect postfire mortality trends. In our stands, higher canopy cover was concurrent with a higher proportion of suppressed and intermediate trees (r = 0.40, p < 0.005). Higher canopy cover could thereby reflect an increased probability of passive crown fire, with smaller trees helping to initiate the movement of fire from surface fuels to the few overstory ponderosa pines that were scorched. These trees suffered one of two fates: in plots with high canopy cover, smaller trees were entirely scorched or incinerated, while all dominant or codominant trees survived their fire injuries.

In contrast to results reported in another analysis of mixed conifer forest mortality (Stephens and Finney 2002), our data supported a significant likelihood estimate for black oak mortality prediction, and we are unaware of any other study that models tanoak survivorship following fire. Diameter did not play a role in the mortality of the two angiosperms, an important differentiating factor from the coniferous species. Overall mortality rates were higher in black oak and tanoak than in the conifers, a trend depicted in two other studies addressing black oak's resistance to fire damage in mixed forests (Regelbrugge and Conard 1993; Hely et al. 2003). Regelbrugge and Conard (1993) found DBH to be a significant predictor of mortality in black oak, based on trees with higher mean DBH and height than those in our study. Authors investigating the allometric relationship between stem size and bark thickness in mixed conifer forest species found that differences in heat tolerance between species <20 cm DBH were slight, even in fire-resistant species (van Mantgem and Schwartz 2003). A significant DBH term in mortality models indicates differential resistance to cambial injury, and is predicated on the assumption that the sample modeled captures a significant range of DBH values and associated bark-related heat tolerance. Mean DBH of black oak and tanoak was 15 and 20 cm, respectively, and highly skewed towards the smaller size classes, suggesting that differential resistance to heating was not yet exemplified by the individuals in our sites.

While bark char severity ratings at maximum bole char heights did not play a significant role, the char severity rating opposite the side of maximum char height produced a strong univariate model for black oak. This measure likely indicates prolonged flame residence near the base of the trees, resulting in a higher degree of stem necrosis and signifying a greater potential for girdling in black oaks because their bark is thinner and denser than that of their coniferous associates (Plumb 1980). This prolonged flame residence explains the relatively greater bole charring at the base of the tree opposite the maximum char height when compared with charring at the highest bole scorch position (Table 2). Bole charring at maximum height was typically a result of a short exposure to flames that reached their maximum height during flame-front passage. The char severity rating was also important for predicting mortality in incense cedar, one of only two species that showed differences in char severity ratings between live and dead trees. In other reports, alternative measures of bole damage, including stem scorch height (Stephens and Finney 2002) and char height (Regelbrugge and Conard 1993), were successful in modeling incense cedar mortality. The role played by each of these measures reveals the susceptibility of smaller incense cedars to cambial damage and girdling, in part because they had thinner bark and higher susceptibility to fire than their coniferous counterparts (Show 1915; Powers and Oliver 1990). In our sample, incense cedars with DBH >25 cm were more likely to survive than die following any level of crown damage, while probabilities of mortality for those <25 cm DBH rose steadily as TCD increased (Fig. 6).

Role of fire intensity in predicting tree mortality

Attempts to relate fire intensity to stem necrosis in two eastern deciduous species proved unsatisfactory, but outpredicted flame-residence time alone when the two measures were combined (Bova and Dickinson 2005). Similarly, fireline intensity by itself did not explain significant variation in tree mortality in our study, but was a significant predictor when paired with tree-morphology parameters such as DBH. In addition, including a term for the consumption of large downed woody fuels decreased the lack of fit and increased ROC and R^2 values in unit 400 (where consumption was highest) as well as for all units merged. Large woody fuels are considered less influential for fire behavior than smaller fuels (van Wagtendonk 1983; Stephens 1998), but appear to be significant in terms of fire effects. If fire intensity and fuel continuity are high enough, and the moisture content of 1000 h fuels is low enough to result in their ignition, they are likely to increase overall flame-residence times and the duration of heat pulses absorbed by nearby vegetation and soils. Greater consumption of these fuels indicates longer periods of either flaming or smoldering combustion, resulting in a greater degree of stem or fine-root damage in proximate trees.

Fire-behavior models such as BEHAVE (Burgan and Rothermel 1984) or FOFEM (Reinhardt et al. 1997) yield estimates of flame length that are used to generate expected ranges of fireline intensity prior to the implementation of prescribed burning. Using these predictions along with DBH, our models would allow a researcher or manager to estimate tree mortality for each tree species and DBH class prior to burning. This contrasts with the majority of logistic regression models that rely on measures of postfire injury for predicting tree mortality. This work can be incorporated into existing fire-severity models, including Fire Management Analyst Plus™ (Carlton 2005), NEXUS (Scott 1999), and FOFEM (Reinhardt et al. 1997), to better estimate potential fire severity in similar mixed conifer forests.

Using replicates in tree-mortality modeling and prescribed burning

Replication of sites is one of the greatest challenges in fire-effects research (van Mantgem et al. 2001). To compensate for the statistical violations presented by lack of replication, post-wildfire studies of fire effects can use similar, unburned reference sites, thereby controlling for background environmental fluctuations (van Mantgem et al. 2001). Experimental or closely managed prescribed burns allow for the collection of prefire data and the approximation of replicated fire events, and provide opportunities for long-term monitoring of fire effects. Where initial stand conditions are similar and stands are independent, prescribed burns can be administered in such a manner that replication is achieved.

In this study, preburn inventories of stand structure and fuel distribution showed no significant differences between the three stands, and in light of similar burning conditions during active ignitions and burnout (Table 1), the prescribed fires could be considered replicates. In addition, firing was modified on steeper slopes, with narrower strip-head fires being used to moderate fire intensities in these areas. As expected, fire intensities were similar in all units (ANOVA, $\alpha > 0.05$), therefore we could examine the consistency of species' responses to the effects of replicated fires. Our analysis of deviance in the postfire mortality models of the two best represented species yielded mixed results. Variability in incense cedar mortality patterns was significantly higher between units than within the combined units. This reveals a differential response of incense cedar to similar burning scenarios. The opposite was true for white fir, where mortality patterns in relation to TCD did not differ significantly between units. Although overall species composition, density, canopy cover, mean DBH, and basal areas were similar in the three sites, analysis at the individual species level unveiled underlying differences. Incense cedar trees were shorter and smaller and TCD was higher in unit 400 (ANOVA, $\alpha = 0.05$). This finding implies that the supposition of similarity among sites at the stand level may not be applicable to an analysis at the species level, and is sensitive to the precision of the data that are used to designate the replicates. Ideally, one could assess fireline intensity at each tree's location, to minimize the impact of highly localized variation in fire behavior and its resulting effects. Especially when the stochastic nature of fire is taken into consideration, the quantification of replication depends on the scale at which a site's components and processes are measured.

Conclusion

The ability to accurately model and interpret potential fire severity is essential in planning and implementing successful treatments of forest vegetation in western coniferous forests. This tenet holds true for treatments with a wide range of goals, including restoration of forest structure and process, commercial production of forest products, and management of vast tracts of publicly owned land to meet sometimes conflicting management objectives.

This work quantifies first-order fire effects, and will be followed by other studies addressing tree mortality in relation to insect activity and disease. The results of this work can be incorporated into existing quantitative models to better predict fire severity across a wide range of species common to the Sierra Nevada and Cascade Ranges of California. These results are best applied to sites that are similar in site class, age structure, species composition, and past management history. Specifically, mixed conifer stands at Blodgett Forest are classified as Dunning site classes I and Ia (Dunning 1942), with relatively young, even-aged stands that were initiated in the early 20th century after intensive railroad logging. Research stands had been thinned from below at least once in the past 20 years, retaining most dominant and codominant trees. We recognize that fire-induced mortality might continue over the next 2–8 years (Ryan et al. 1988), potentially changing the species' response patterns reported here. Longer term responses to the prescribed burns will be monitored in hopes of addressing the effects the burns may have had on tree vigor and resistance to any additional stressors.

Our analysis of replication of the prescribed burns revealed some limitations that are already largely accepted in fire-effects studies. The importance of fine-scale factors in dictating fire behavior and individual species' responses likely explain the discrepancy in mortality patterns between white fir and incense cedar that we found. A continuance of attempts to standardize fire-effects research should help decrease bias, improve comparability between studies, and work towards a consensus on applicable statistics and essential study-design criteria.

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