

Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest

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Abstract

Over the last century, fire exclusion in the forests of the Sierra Nevada has allowed surface fuels to accumulate and has led to increased tree density. Stand composition has also been altered as shade tolerant tree species crowd out shade intolerant species. To restore forest structure and reduce the risk of large, intense fires, managers have increasingly used prescription burning. Most fires prior to EuroAmerican settlement occurred during the late summer and early fall and most prescribed burning has taken place during the latter part of this period. Poor air quality and lack of suitable burn windows during the fall, however, have resulted in a need to conduct more prescription burning earlier in the season. Previous reports have suggested that burning during the time when trees are actively growing may increase mortality rates due to fine root damage and/or bark beetle activity. This study examines the effects of fire on tree mortality and bark beetle attacks under prescription burning during early and late season. Replicated early season burn, late season burn and unburned control plots were established in an old-growth mixed conifer forest in the Sierra Nevada that had not experienced a fire in over 120 years. Although prescribed burns resulted in significant mortality of particularly the smallest tree size classes, no difference between early and late season burns was detected. Direct mortality due to fire was associated with fire intensity. Secondary mortality due to bark beetles was not significantly correlated with fire intensity. The probability of bark beetle attack on pines did not differ between early and late season burns, while the probability of bark beetle attack on firs was greater following early season burns. Overall tree mortality appeared to be primarily the result of fire intensity rather than tree phenology at the time of the burns. Early season burns are generally conducted under higher fuel moisture conditions, leading to less fuel consumption and potentially less injury to trees. This reduction in fire severity may compensate for relatively modest increases in bark beetle attack probabilities on some tree species, ultimately resulting in a forest structure that differs little between early and late season prescribed burning treatments.

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1. Introduction

Prior to the past century of fire exclusion, frequent fire had long been a major ecosystem influence in California's Sierra Nevada mixed-conifer forests (Swetnam and Baisan, 2003). The introduction of grazing, decimation of the Native American population, and more recent fire suppression policies however, resulted in fire exclusion and increased tree density, fuel accumulation, and fuel continuity on the forest floor (Skinner and

Chang, 1996; McKelvey and Busse, 1996; Bradley and Tueller, 2001). Fire exclusion has promoted uniform tree age and structural distributions, and has altered stand composition by allowing shade tolerant species such as firs (*Abies*) to crowd out shade intolerant species such as pines (*Pinus*) (Parsons and DeBenedetti, 1979; Barbour et al., 2002). The unnatural accumulation of fuels and changes to stand structure are feared to have detrimental effects on the ecosystem while also greatly increasing the risk of high intensity crown fires.

As knowledge of the negative effects of fire suppression has grown, managers have increasingly relied on prescribed fire to reduce fuel loads and restore natural ecosystem processes

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(Kilgore, 1973; Kilgore and Sando, 1975; Keeley and Stephenson, 2000; Stephens and Ruth, 2005). Historically, wildfires in the Sierra Nevada occurred most frequently in the late summer and early fall (Caprio and Swetnam, 1995) when fuels are driest and trees dormant or nearly so. Late season prescribed burning has been favored by some managers because it approximated the historical fire season and the onset of fall precipitation can reduced post-fire monitoring for escapes. However, the fall burning season often coincides with stable atmospheric conditions when smoke dispersal is poor (Cahill et al., 1996) and managers face increased legal restrictions on burning. As a result, an increasing number of prescribed burns are being conducted during the early season when atmospheric conditions are more favorable for smoke dispersal.

Most pre-EuroAmerican settlement fires occurred in late season. The potential differences in tree mortality from fires in late spring or early summer rather than in the late summer or fall are still not well understood and reports in the literature have been contradictory. On one hand, early season burns occur at the beginning of the annual growth period and plants have been shown to be more susceptible to heat damage when carbohydrate reserves are at their lowest levels (Hough, 1968; Garrison, 1972). For example, growing season prescribed burns have resulted in greater ponderosa pine (*Pinus ponderosa*) mortality than dormant season burns (Swezy and Agee, 1991; Harrington, 1993). Damage to fine roots that are abundant in the litter and duff layers, particularly during the early season period of tree growth, may be an explanation (Swezy and Agee, 1991). On the other hand, late season burns are likely to be of greater intensity because fuels are typically drier (Skinner and Chang, 1996), and a recent replicated experiment in eastern Oregon ponderosa pine forests revealed greater mortality following late season burns (Thies et al., 2005).

Trees weakened by fire are susceptible to attack by insects such as bark beetles. Season of fire might influence tree mortality by affecting this susceptibility according to the time of year when the damage occurs—trees damaged when carbohydrate reserves are low may be unable to defend against attack (McCullough et al., 1998; Goyer et al., 1998; McHugh et al., 2003). In the Sierra Nevada, bark beetles (Coleoptera: Scolytidae) are common pests that kill firs and pines, and are capable of large-scale population increases following disturbances such as droughts or fires (Miller and Keen, 1960; Bradley and Tueller, 2001). Such outbreaks can be in response to tree physiological conditions that enable insects to circumvent tree defenses (Berryman, 1982; Mattson and Haack, 1987; Logan et al., 2003; Wallin et al., 2004), or in response to physical and structural attributes of conifer stands that favor bark beetle populations (Sanchez-Martinez and Wagner, 2002; Sartwell and Stevens, 1975; Mitchell et al., 1983; Powers et al., 1999). Dense forests subject to fire exclusion are feared particularly susceptible to insect attack (Wallin et al., 2004; Sala et al., 2005).

Bark beetle attacks are expected to increase in response to weakened tree defenses following fires (Ryan and Amman, 1994; McHugh et al., 2003), and one prediction is that fires resulting in more severe effects on trees will produce more resources for bark

beetles. However, individual trees within a species vary in their suitability as hosts (Rudinsky, 1962; Wright et al., 1979; Wallin et al., 2004) and some previous work has suggested that bark beetle preference for trees may be a “humped-shaped” response to tree health: vigorous trees and very damaged trees both provide poor resources (Mitchell et al., 1983). An open question is the extent to which bark beetle attacks and resulting secondary mortality follow or differ from the pattern of primary fire-caused mortality. Differences in fire behavior due to environmental conditions at the time of burning may result in different effects on tree defenses against bark beetles with fire season. The timing of fires might also influence bark beetle activity through direct effects on beetle populations and phenology: late season burns occur after bark beetle activity has ceased for the season and may provide fewer wounded but suitable trees available for bark beetles the following spring.

The purpose of this study was to evaluate the differences in direct and secondary tree mortality with early season and late season prescribed fires. This study was intended to provide managers with information to tailor prescribed burning operations so that both fuel reduction and forest stand structure and composition restoration goals are met.

2. Methods

2.1. Study sites and system

This study was located in an old growth mixed conifer forest within the Marble Fork watershed of the Kaweah River, Sequoia National Park, CA, USA. To test for the effects of fire season on tree mortality and bark beetle activity, three treatments (early season, late season, and unburned control) were applied to nine experimental units in a completely randomized design. Each treatment was replicated three times. The experimental units were each 15–20 ha in size and were located on west to northwest facing aspects of variable slope at elevations ranging from 1900 to 2150 m above sea level. Prior to the burns, the most common tree species were white fir (*Abies concolor* Gordon and Glend.), sugar pine (*Pinus lambertiana* Douglas), and incense cedar (*Calocedrus decurrens* Torrey). Red fir (*A. magnifica* Murray), Jeffrey pine (*P. jeffreyi* Grev and Balf.), ponderosa pine (*P. ponderosa* Lawson), mountain dogwood (*Cornus nuttallii* Audobon), and black oak (*Quercus kelloggii* Newb.) were also present at low densities.

2.2. Fire history

To establish the historical fire return interval and season during which fires burned, we collected cross sections of snags and logs containing fire scars at four locations within or adjacent to the study area. Each collection location was approximately 2 ha in size, and between five and nine fire scarred snags or down logs were sampled per location. The majority of cross sections were from *P. lambertiana*, but some *P. jeffreyi* and *C. decurrens* sections were also used. Cross sections were sanded to improve visibility of the annual rings. Fire scars were identified and fire years determined by cross-dating, using standard

dendrochronological techniques (Stokes and Smiley, 1968; Swetnam et al., 1985). Composite fire histories were constructed and mean fire return interval and season of burning statistics were calculated for each collection location using the FHX2 software package (Grissino-Mayer, 2001). Other evidence of fire, such as the presence of resin tubes (Brown and Swetnam, 1994) was used in addition to fire scars, but only when a fire scar was found in other trees at the same location in the same year. Scars and other fire damage prior to 1630 were not used due to lack of sufficient material with clearly visible fire scars before this time. Only scars noted on at least two trees per collection location were considered in the calculation of average fire return interval. Season of fire occurrence was noted by the location of the fire scar within the annual growth ring (method described in Caprio and Swetnam, 1995).

2.3. Treatments

Early season burns were conducted on 20 and 27 June 2002. Late season burns were conducted on 28 September, and on 17 and 28 October 2001. Ignition of each unit was started at the highest point in the unit, and accomplished with drip torches. Burns were strip head fires of low to moderate intensity. Except for a few cases of individual trees torching, fire was predominantly on the surface. Weather and fuel conditions at the time of the burns are provided in Knapp et al. (2005).

2.4. Tree mortality survey

All pre- and post-treatment data were taken in plots referenced to a set of 36 points established on a 50 m grid in the interior of each unit. To minimize edge effects, the grid system was surrounded by a 50–100 m buffer that was also treated. Tree survival data were collected within 20 m × 50 m (0.1 ha) modified Whittaker plots, 10 of which were established per unit. Plots were randomly located in reference to the network of 36 permanent points. The grid point formed one corner of the 20 m × 50 m plot, and placement of the plot in one of the four cardinal directions was also random. Within plots, all trees with a diameter at breast height (DBH) greater than 10 cm were labeled with a uniquely numbered tag. Smaller diameter trees were not permanently tagged and were therefore not included in the estimates of mortality probability. Tree species was determined, status (alive, standing dead, dead and down) was noted, and DBH was measured. Units were sampled in 2001 prior to treatment, in 2002 (immediately post treatment) and in 2004, the final year of the study.

2.5. Fire intensity measures

Two measures of fire intensity are reported in this paper: tree crown scorch height and height of bole charring. Both correlate with fire intensity and have been shown to influence tree mortality (Alexander, 1982; Peterson and Ryan, 1986; Ryan and Reinhardt, 1988). Crown scorch height was measured on all trees within plots using a laser range finder and was calculated as the average of two measurements: the maximum scorch height and

scorch height on the opposite side of the tree of where maximum scorch height occurred. Height of bole charring was measured similarly (average of maximum and side opposite).

2.6. Bark beetle survey

We measured the intensity of bark beetle attacks and resulting secondary mortality in all units following the prescribed burns. Fir and pine associated bark beetles co-occur in the mixed-conifer forests of the Sierra Nevada. Other tree species, which occur at low densities and are not attacked by bark beetles, were excluded from the bark beetle analysis.

The fir engraver beetle, *Scolytus ventralis* LeConte, feeds exclusively on the genus *Abies*; two *Abies* species *A. concolor* and *A. magnifica* were in the study units, with the latter mainly at the highest elevations. The red turpentine beetle, *Dendroctonus valens* LeConte, feeds on all pines present in the study sites. Mountain pine beetle, *D. ponderosae* Hopkins, feeds on *P. lambertiana* and *P. ponderosa*, while *D. jeffreyi* is monophagous on *P. jeffreyi*. A number of other tree damaging Scolytids (especially *Ips* species) occur in this system, but were rare at the time of the surveys.

Trees were surveyed for bark beetles at each of the 36 points on the 50 m grid system. A 180° half-circle survey was performed to the north of each grid point during June and July 2003. A second survey, using the same methodology, was performed in June 2004. Due to the large difference between *Abies* and *Pinus* densities, all *Pinus* within a 25 m radius half circle, and all *Abies* within a 12.5 m radius half circle were examined for evidence of pitch tubes and other evidence of bark beetle attack. Trees that died following the fire treatments were also examined for the presence of both pitch tubes and bark beetle galleries by removing bark from at least two locations on the lower bole. Beetles were identified by pitch tube shape and location and distinguished by gallery characteristics. Additionally, live or dead beetles were often found and collected. When bark beetle evidence was noted, beetle species, tree species, and tree DBH were recorded. Trees within the survey area not exhibiting evidence of bark beetle attack were also recorded by species and DBH. It is possible that evidence for *Ips* which may only be signaled by the presence of boring dust might be missed, especially if attacks occurred high on the tree bole or evidence was obscured by subsequent colonization by other beetles. *Ips* were found on only five trees in the study and are not included in the analysis. Additionally, a pilot trapping survey in 2003 in the plots using sticky cards on trees at breast height and Lindgren funnel traps (Phero Tech Inc., Delta, BC, Canada) failed to capture a single *Ips*, but all other species of beetle mentioned were captured (unpublished data).

2.7. Analyses

Data were collected at two scales: intensive data on many variables was collected in the 20 m × 50 m vegetation plots and less detailed information was collected in the more spatially extensive bark beetle survey. For analysis of fire-caused

mortality and the effect of fire intensity, we used the vegetation plot data. For assessing bark beetle attacks and subsequent tree mortality, we used the bark beetle survey.

To test for treatment effects we used analysis of variance on the unit-level summaries. To investigate changes in stand structure we used ANOVA to test changes in tree basal area and density before and after the treatments. To compare probabilities (bark beetle attack probability and mortality probability) we used the arcsine square root transformed probabilities calculated from proportions. In our nested model (tree size class nested within experimental unit), we compared unit-level means and tested for a priori contrasts among the three treatments: first, for effect of burning and second, for an effect of season of burn.

For analyzing bark beetle attacks and tree response by treatment, separate models were used for *Abies* and for *Pinus*. Few new bark beetle attacks were found in 2004, and bark beetle data for 2003 and 2004 were therefore combined for this analysis: that is, trees that showed evidence of attack in 2003 or 2004 were scored as ‘attacked’ by that beetle species. The number of *A. magnifica* in the study area was small in relation to the number of *A. concolor*, and since *S. ventralis* can use and kill both *Abies* species, analyses of attacks and mortality associated with *S. ventralis* were performed on the combined *Abies* species. Attacks and associated mortality from all bark beetle species on the three *Pinus* species were analyzed together to characterize the overall secondary mortality following fire in this forest. Attacks on *Pinus jeffreyi* and *P. ponderosa* could not be analyzed separately because these species were not found in all experimental units. *Pinus lambertiana*, on the other hand, which occurred in all nine experimental units and is of special interest because of population declines, was analyzed separately. Because *D. valens* alone do not typically result in tree death, attack probability and conditional probability of tree mortality given an attack were analyzed separately for *D. ponderosae* and *D. valens* attacks. *Calocedrus decurrens* is not attacked by bark beetles and was omitted from the bark beetle survey.

At the vegetation plot level, we investigated the potential effect of fire intensity measures using binomial (logistic) regression. Logistic regression was used to model the response of tree mortality to bole char and crown scorch as a measure of fire intensity. The intensity effects on secondary mortality (post-fire to 2004) were compared to the same effects on direct post-fire mortality. Data used were the vegetation plot mortality proportions for burned treatments, weighted by number of trees for *Pinus* and *Abies* separately. Analyses were conducted with the glm procedure in R (R Development Core Team, 2005).

3. Results

3.1. Fire history

The average fire return interval for the sampled locations in the study area was 27 years, with a range of 7–56 years (Fig. 1).

Over the entire approximately 4 km² study area a fire occurred on average every 16 years (range of 1–26 years between subsequent fires (composite at the bottom of Fig. 1)). Three fires burned across all four sites in the same years: 1729 (19 samples), 1777 (23 samples), and 1879 (20 samples). The last fire recorded was in 1879. There is a weak fire frequency gradient among the sites from low-to-high elevation (west to east) that is similar to that found elsewhere in the Kaweah watershed (Caprio and Swetnam, 1995; Caprio, 2004). The overwhelming majority of fires prior to EuroAmerican settlement burned in the late season. Of the fire scars that could be reliably categorized by season, 89% were found in the late wood or at the dormant ring boundary and only 11% were in early wood (2% in early-early wood, 3% in mid-early wood, and 6% in late-early wood).

3.2. Direct tree mortality and overall effects on stand structure

The size distribution of trees was affected by burning treatments with a shift towards larger size classes in 2002 compared to 2001. Secondary mortality strengthened this pattern with an increased shift towards larger DBH through the loss of smaller trees. Quadratic mean DBH increased significantly over the course of the study for both genera in the burn treatments relative to the controls (ANOVA, $p < 0.001$). Table 1 shows the mean basal area/ha and densities of trees by treatment in 2001 and 2004 for comparison with other studies.

ANOVA examination of the change in tree density and basal area between 2001 and 2002 showed that both burning season treatments resulted in significantly reduced tree density and basal area relative to controls (ANOVA, $n = 9$, d.f. = 2, $p = 0.005$, Table 1), but a significant difference between early and late season burns was not found ($p = 0.22$).

Two-way ANOVA on mortality response to treatment and tree size class (size class nested within experimental unit) showed a significant effect of burning and size class for initial fire-caused mortality (Fig. 3, treatment $F_{2,3} = 5.61$, $p = 0.040$; size class $F_{2,3} = 22.0$, $p < 0.001$). ANOVA on the total mortality by size class and treatment over the course of the study (2001–2004) also showed a significant effect of burning and size class (treatment $F_{2,3} = 17.6$, $p = 0.003$; size class $F_{2,3} = 56.9$, $p < 0.001$). Neither initial nor total (initial plus secondary) mortality differed significantly between burning seasons, although there was a tendency for mortality to be higher in the late season burns. These patterns were very similar for all tree species.

We used the geometric mean of crown scorch height (m) and bole char height (m) as a simple measure of fire intensity. Logistic regression was used to model the effect of vegetation plot mean intensity on proportion of trees killed directly by fire. Fire intensity significantly influenced proportion of trees killed by fire but was not a significant effect on secondary mortality, although for pines there was a trend for increasing secondary mortality with increasing intensity (Fig. 2, Table 2). This measure of mean fire intensity did not differ significantly between early and late season burns ($F_1 = 1.18$, $p = 0.34$).

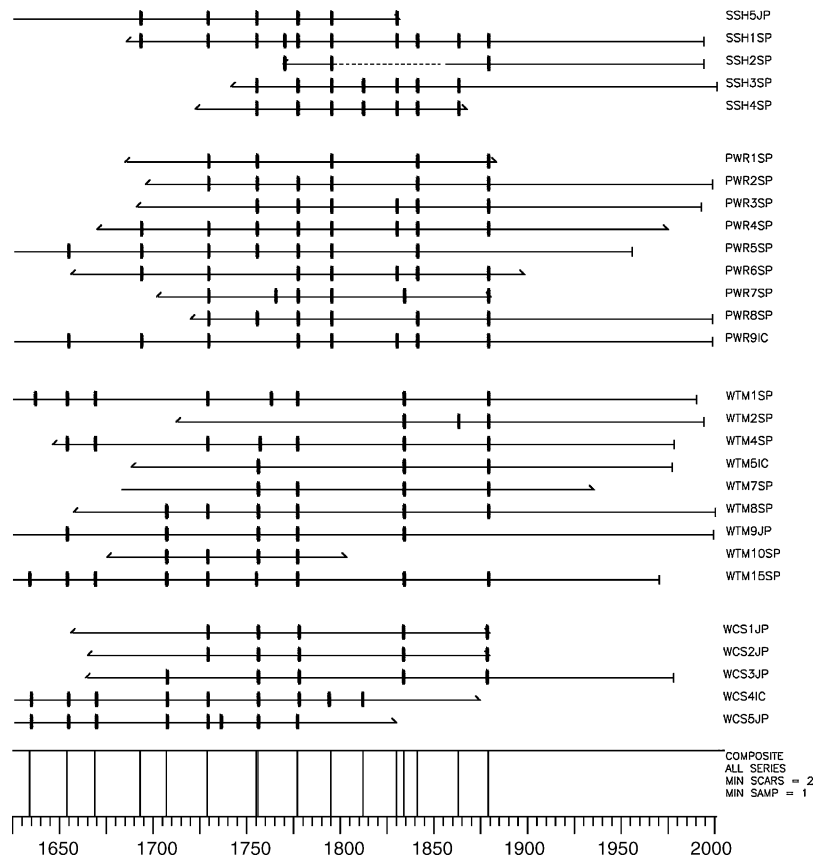


Fig. 1. Fire history of the study area in Sequoia National Park. Data from the four fire scar collection locations are separated by a space. Sites are arranged from west-to-east (top-to-bottom in the figure). Each horizontal line is the record from a single tree. Recorder years are designated with a solid line and null years where tree ring clarity was not sufficient to determine fire scar dates are designated with a dashed line. Each bold vertical line represents a year with a fire scar. The composite at the bottom of the figure shows fires recorded by a minimum of two trees per location.

Among plots, there was a significant correlation between direct fire-caused mortality and secondary mortality ($r^2 = 0.095$, $p = 0.010$).

3.3. Bark beetle attacks

Bark beetle attacks on both *Abies* and *Pinus* species were more frequent in burned plots than in the controls. For *Abies*, attacks were more frequent following early season burns than following late season burns (Fig. 4, Table 3). For *Pinus*, there

was no significant effect of season on attack probabilities. Unlike attacks on *Abies*, attacks on *Pinus* were common both on large and small trees (Fig. 4), but a significant portion of bark beetle attacks on larger pines was due to *D. valens*, which does not generally kill attacked trees (Fig. 5).

The probability of mortality for attacked trees was greater for small *Abies* than for large *Abies* (Fig. 4). For *P. lambertiana* with *D. ponderosae* attacks, there was no difference in probability of mortality with bark beetle attack between small and large trees (Table 4). We divide trees into only two size

Table 1
Mean basal area and tree density for trees with a DBH (1.37 m) >10 cm by treatment in 2001 (pre-treatment) and 2004

Measurement	Treatment (year)					
	Control		Early		Late	
	2001	2004	2001	2004	2001	2004
Basal area ($\text{m}^2 \text{ha}^{-1}$)	59.3 ± 2.6	60.6 ± 2.9	65.3 ± 1.7	55.0 ± 7.2	64.7 ± 8.00	53.6 ± 8.5
Density (trees/ha)	320.0 ± 35.0	319.0 ± 34.1	407.0 ± 21.3	254.0 ± 67.0	325.2 ± 15.0	146.0 ± 39.0
Density of saplings	243.3 ± 84.6	248.0 ± 97.1	352.0 ± 56.3	177.3 ± 128.5	390.0 ± 164.4	86.2 ± 34.0
Basal area of <i>Abies</i>	44.1 ± 11.9	45.0 ± 12.1	37.5 ± 6.8	34.2 ± 6.8	42.4 ± 14.52	37.1 ± 15.3
Density of <i>Abies</i>	218.7 ± 68.8	221.7 ± 72.2	240.3 ± 65.9	154.7 ± 64.1	220.0 ± 48.4	109.3 ± 55.2
Basal area of <i>Pinus</i>	8.1 ± 4.9	8.3 ± 5.1	16.3 ± 1.7	11.6 ± 1.4	15.9 ± 9.4	12.1 ± 6.5
Density of <i>Pinus</i>	42.7 ± 20.0	39.1 ± 17.3	67.3 ± 23.4	36.0 ± 4.3	61.3 ± 27.3	23.7 ± 8.5

Density of trees <10 cm DBH (saplings) are also shown, although these small trees were not permanently tagged and were not used in mortality estimates. Means are shown ± standard deviation. These are the untransformed data values for comparison with other studies.

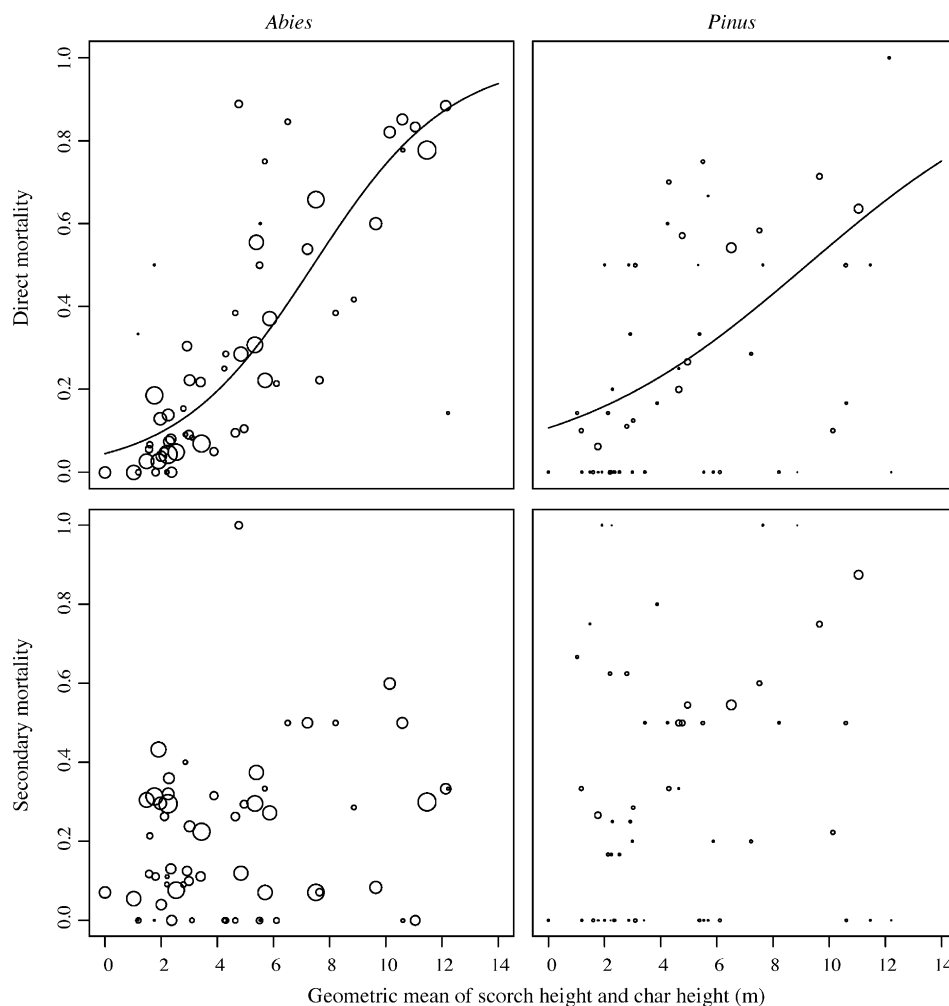


Fig. 2. Initial tree mortality following fire and secondary tree mortality (2002–2004) in response to fire intensity: geometric mean of average plot crown scorch height (m) and average plot bole char height (m). Lines in the upper panels show predicted values from logistic regression (Table 2). Each circle represents a vegetation plot and symbol sizes are proportional to the logistic regression weights (number of trees comprising the proportion).

classes here for simplicity and to increase within-plot sample size because graphical investigation revealed 40 cm DBH as the transition point for attack probabilities. There was no difference between early and late season burns on the conditional probability of mortality given an attack. Mortality of *Pinus* attacked by *D. valens* alone was essentially zero. The other pine species occur in much lower numbers and cannot be tested statistically, but mortality rates in attacked *P. ponderosa* and *P. jeffreyi* tended to be higher in smaller trees. There was no

significant relationship between vegetation plot basal area and probability of bark beetle attack.

4. Discussion

Although land managers often schedule burning according to safety and logistical priorities, there is concern that burning outside of the natural fire season may have unwanted effects in many ecosystems (Swezy and Agee, 1991; Harrington, 1993;

Table 2

Binomial logistic regression parameters: direct tree mortality as a response to fire intensity (geometric mean of crown scorch height (m) and bole char height (m)) as plotted in Fig. 2

Response	<i>a</i>	<i>b</i>	S.D. <i>b</i>	Null deviance	Residual deviance	d.f.	<i>p</i>
Direct mort. (<i>Abies</i>)	−3.1	0.41	0.024	584.3	178.2	58	<0.001
Direct mort. (<i>Pinus</i>)	−2.1	0.23	0.036	15.9	116.0	54	<0.001
Secondary mort. (<i>Abies</i>)	−1.57	−0.048	0.031	143.8	141.6	58	0.12
Secondary mort. (<i>Pinus</i>)	−0.997	0.079	0.041	113.7	110.2	53	0.061

Predicted lines take form: $p = 1/(1 + e^{-(a+bx)})$. Experimental unit was treated as a random effect in the binomial model analysis.

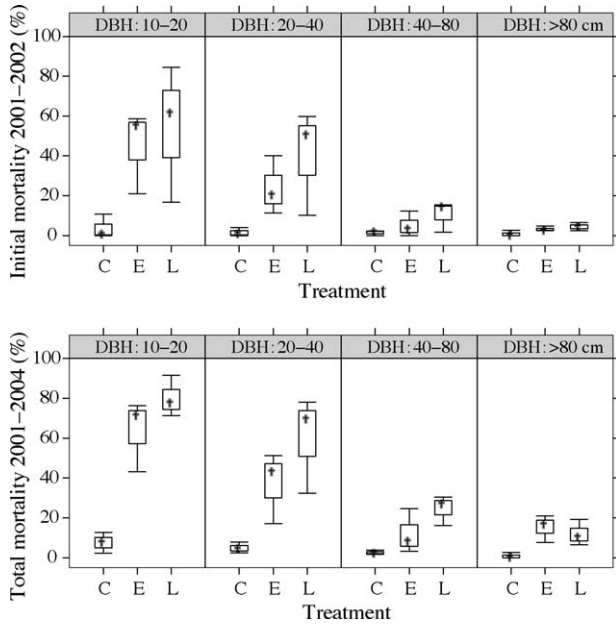


Fig. 3. Initial tree mortality following fire (top panel) and total tree mortality over the experiment (bottom panel) by size class and treatment. Box plots show median (dot), 25–75th quantiles (rectangle), and range (whiskers). Data presented in the figure are vegetation plot means; statistical tests were carried out at the level of replication (experimental units).

Drewa et al., 2002). Early season burning in Sequoia National Park, however, does not appear to be completely out of the seasonal range of pre-EuroAmerican settlement fires. An ongoing study of tree growth very near these sites shows that radial size increase begins in late May or early June and continues until mid-July (Caprio, unpublished data). According to a study of radial growth of trees in the Sierra Nevada at

Table 3

Mean bark beetle attack probabilities for *Abies* and *Pinus* by treatment

Genus	Attack probability			Significance by contrast		
	Control	Early	Late	Burning	Season	Overall
<i>Abies</i>	0.018	0.256	0.121	<0.001	<0.001	<0.001
<i>Pinus</i>	0.155	0.449	0.494	<0.001	0.32	<0.001

p-Values are based on results from ANOVA using the arcsine square root transformed probabilities. The overall treatment effect as well as two priori contrasts were tested.

similar elevations to the study area by Fowells (1941), early season fire scars should correspond to growth between late May to late July, while late season scars should correspond to wood added in August and beyond. The early season prescribed fires in this study would likely have corresponded to early-early or mid-early fires according to the convention used to describe fire scar season in Fowell’s, 1941 study. The fire scar records indicate that approximately 95% of fires at the study site historically occurred later than this.

The average fire return interval (27 years, Fig. 1) in the study area is slightly longer than values reported previously from nearby locations in Giant Forest: Caprio and Swetnam (1995) found an average fire return of 23 years for eight collection locations. Variation in fire regime with aspect has been demonstrated in other studies and attributed to differences in fuel production, fuel moisture, and fuel structure (Taylor and Skinner, 1998; Beatty and Taylor, 2001; Taylor and Skinner, 2003; Caprio, 2004). Northwest facing slopes like those in this study may have burned less often because of a shorter period when fuels are dry (Caprio and Graber, 2000) and contain a greater abundance of firs, which produce a dense litter-bed

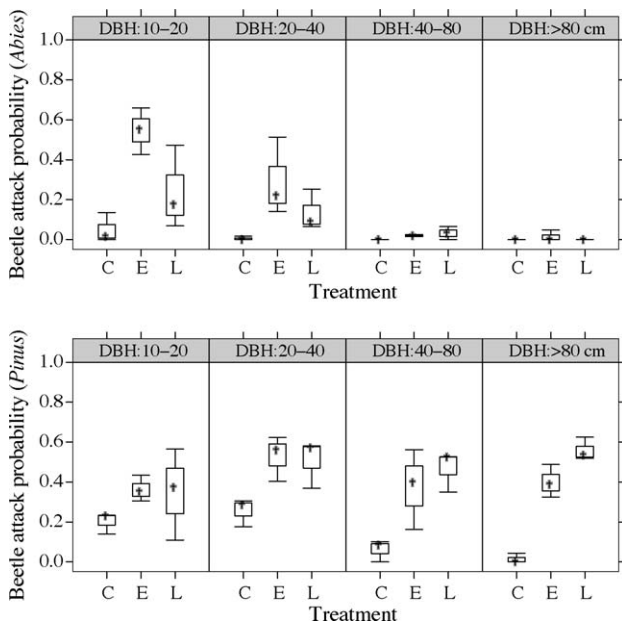


Fig. 4. Bark beetle attack probabilities for *Abies* (top panel) and *Pinus* (bottom panel) by treatment and tree size class. Box plots show median (dot), 25–75th quantiles (rectangle), and range (whiskers).

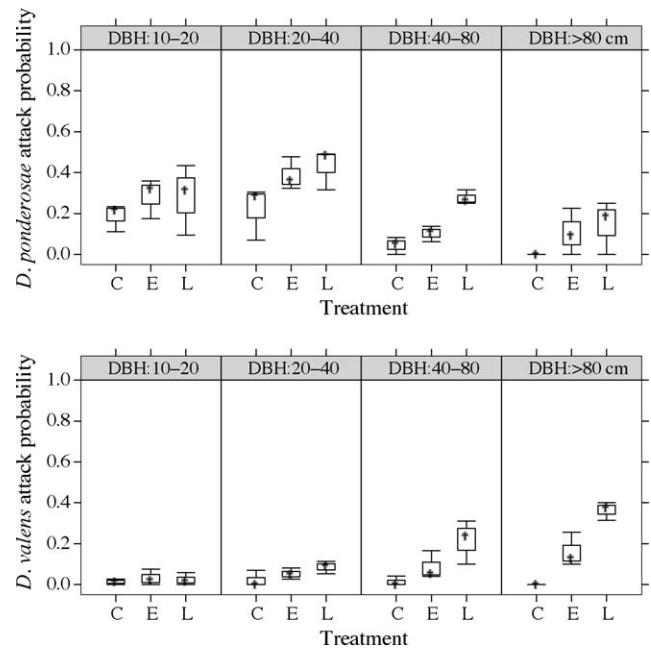


Fig. 5. *D. ponderosae* (top panel) and *D. valens* (bottom panel) attack probabilities on *Pinus* by treatment and tree size class. This probabilities did not differ significantly by season (data not shown). Box plots show median (dot), 25–75th quantiles (rectangle), and range (whiskers).

Table 4
Mean tree mortality probabilities by size class for *Abies* and *Pinus* given the presence of a bark beetle attack

Genus	Mortality probability given attack		<i>p</i>
	DBH 10–40 cm	DBH >40 cm	
<i>Abies</i>	0.88	0.50	0.044
<i>P. lambertiana</i>	0.83	0.78	0.22

Data are shown for attacks on *Abies* by the fir engraver (*Scolytus ventralis*) and for attacks on *P. lambertiana* by mountain pine beetle (*D. ponderosae*). *p*-Values for the size class effect are based on results from ANOVA using the arcsine square root transformed probabilities.

(Stephens et al., 2004) that can reduce fire intensity and hamper fire spread (Fonda et al., 1998). The fire dates for the years 1729 and 1777 are found throughout much of the Kaweah watershed (Caprio and Swetnam, 1995; Caprio, 2004) and are related to years of below average reconstructed precipitation (Swetnam, 1993; Swetnam et al., 1998).

Although several previous studies have suggested that burning in the early season may have more severe effects on trees than burning in the late season (Harrington, 1987, 1993; Swezy and Agee, 1991; McHugh et al., 2003), there was no evidence that early season burns resulted in increased direct mortality in this study. Fire intensity significantly influenced tree mortality (Fig. 2, Table 2), but above-ground intensity measured by crown scorch and bole char did not differ significantly between seasons.

Although we did not detect a difference in above ground fire intensity between early and late burns, an investigation of surface fuels in this same experiment by Knapp and Keeley (2006) showed that late season burns were generally more homogeneous than were early season burns. Additionally, early season burns also consumed less litter and duff and burned less of the ground surface than late season burns (Knapp et al., 2005). Soil heating and below ground fire severity may not correlate well with above ground fire intensity and heat produced in the early season burns may not have penetrated as deep into the soil due to higher soil moisture levels (Hartford and Frandsen, 1992; Busse et al., 2005). It is therefore possible that the late season burns had more severe effects on tree root systems and that this greater intensity counteracted any possible effect of increased root susceptibility to damage when trees are growing early in the season. Late season burns consumed more duff during smoldering combustions (Knapp et al., 2005), potentially leading to greater heat penetration. Our mortality results are in general agreement with recent work by Thies et al. (2005), who found greater *P. ponderosa* mortality following late season burns in eastern Oregon.

The increase in bark beetle attacks and associated mortality on both *Abies* and *Pinus* following fire was not unexpected. Bark beetle attacks, however, occurred in the Control units as well. The study area was experiencing a low-level background bark beetle outbreak during the study (personal observation, A.C. Caprio). White pine blister rust (*Cronartium ribicola* J.C. Fisch.) has attacked many *P. lambertiana* in this forest and throughout the Sierra Nevada (van Mantgem et al., 2004), and weakening of infected trees may have contributed to

susceptibility to bark beetle attack as well as to the generally high levels of mortality witnessed in *P. lambertiana*. Work in a variety of systems has generally shown that measures of fire intensity are positively associated with tree susceptibility to attack (Ryan and Amman, 1994; Sullivan et al., 2003; Wallin et al., 2003). In our study, fire intensity as measured by crown scorch height and bole char height had positive effects on direct tree mortality but effects on secondary mortality were not significant.

Continued mortality during the second and third years following the fires increased the total mortality in the burn treatments by approximately 10% for all size classes (Fig. 3). Almost all secondary mortality was associated with bark beetle attacks, although there was occasional mortality on non-attacked trees (such as mechanical failure caused by burned out fire scars at the tree base). Although our study is of longer duration than many, it may not capture all fire-related mortality: previous work has shown that mortality after fire may not reduce to background rates for five or more years (Mutch and Parsons, 1998; van Mantgem et al., 2003).

The increase in *Scolytus* attacks on *Abies* with early season burns was the only adverse affect found to be greater in early season burns compared to late season. It is possible that the increase in attacks on *Abies* in early season is a result of background *Scolytus* populations and an artifact of the size of our experimental units and the timing of the treatments: the early season burns occurred after the late season burns and burn units were located relatively close together. In this scenario, the *S. ventralis* populations may have increased in abundance following the increase in resources after the late season burns and thus the background abundance of bark beetles may have been higher immediately following the early season burns than immediately following the late season burns. Higher beetle densities then may have resulted in more successful attacks on trees. It is also possible that the early season burns provides a resource better timed to bark beetle flight activity (Fettig et al., 2004).

Dendroctonus attacks on *Pinus* did not differ significantly between burn seasons. Fire-caused wounding is but one component that determines the success or the initiation of bark beetle attacks following burns. Tree physiology is also responsive to structural conditions of forest stands, particularly tree density. Over-stocked stands are often considered more susceptible to bark beetle attacks than are open stands (Sartwell and Stevens, 1975; Mitchell et al., 1983), but although dense stands may provide more weakened trees, these trees may not be a preferred resource for *Dendroctonus* beetles. *D. ponderosae*, for example, has been noted to exhibit a “hump-shaped” infestation response to stand basal area in lodgepole pine (*P. contorta*) (Mitchell et al., 1983). We found no relationship between stand basal area and *D. ponderosae* attacks, however.

Prescribed burning in this forest is aimed at decreasing the density of small trees and preserving the larger trees. By this measure, burning in early or late season seem similarly successful. Burning in the early season does not result in generally higher tree mortality compared to late season. In fact, although the mortality differences were statistically

insignificant, mortality tended to be higher in late season burns which consumed more fuel and may have caused greater soil heating (Knapp et al., 2005). In general, secondary mortality during 2002–2004 followed the pattern of direct fire-caused mortality: more trees died as a result of bark beetle attack in plots where initial tree mortality caused by crown scorch was greatest. The exception to this pattern was bark beetle attacks on small *Abies*, which were more frequently attacked in early season burns. This increase in attacks on small *Abies*, however, did not change the general pattern of *Abies* mortality which did not vary significantly with season of burn. If the goal of re-introducing fire into these forests is to reduce the dominance of *Abies* as well as change overall structure and fuel loads, then early season burns which result in greater bark beetle attacks and mortality on small *Abies* relative to other tree species may help achieve these goals.

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