



Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in Ponderosa and Jeffrey Pine Forests in California, USA[☆]

Christopher J. Fettig^{a,*}, Stephen R. McKelvey^a, Daniel R. Cluck^b, Sheri L. Smith^b, William J. Otrrosina^c

^a Pacific Southwest Research Station, USDA Forest Service, 1731 Research Park Drive, Davis, CA 95618, USA

^b Forest Health Protection, USDA Forest Service, 2550 Riverside Drive, Susanville, CA 96130, USA

^c Southern Research Station, USDA Forest Service, 320 Green Street, Athens, GA 30602, USA

ARTICLE INFO

Article history:

Received 30 January 2010

Received in revised form 24 March 2010

Accepted 16 April 2010

Keywords:

Dendroctonus

Fire hazard

Forest restoration

Ips

Pinus jeffreyi

Pinus ponderosa

ABSTRACT

Many forests that historically experienced frequent low-intensity wildfires have undergone extensive alterations during the past century. Prescribed fire is now commonly used to restore these fire-adapted forest ecosystems. In this study, we examined the influence of prescribed burn season on levels of tree mortality attributed to prescribed fire effects (direct mortality) and bark beetles (Coleoptera: Curculionidae, Scolytinae) (indirect mortality) in ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., and Jeffrey pine, *Pinus jeffreyi* Grev. and Balf., forests in California, USA. A total of 816 trees (9.9% of all trees) died during this 3-yr study. Significantly higher levels of tree mortality (all sources) occurred following early and late season burns compared to the untreated control, but no significant difference was observed between burn treatments. The majority (461 trees) of tree deaths were attributed to direct mortality from prescribed burns and was strongly concentrated (391 trees) in the smallest diameter class (<20.2 cm diameter at breast height, dbh). For the largest trees (>50.7 cm dbh), significantly higher levels of tree mortality occurred on early season burns than the untreated control, most of which resulted from indirect mortality attributed to bark beetle attacks, specifically western pine beetle, *Dendroctonus brevicomis* LeConte, and mountain pine beetle, *D. ponderosae* Hopkins. Red turpentine beetle, *D. valens* LeConte, was the most common bark beetle species found colonizing trees, but tree mortality was not attributed to this species. A total of 355 trees (4.3% of all trees) were killed by bark beetles. *Dendroctonus brevicomis* (67 trees, 18.9%) and *D. ponderosae* (56 trees, 15.8%), were found colonizing *P. ponderosa*; and Jeffrey pine beetle, *D. jeffreyi* Hopkins, was found colonizing *P. jeffreyi* (seven trees, 2.0%). We also found pine engraver, *Ips pini* (Say) (137 trees, 38.6%), and, to a much lesser extent, *Orthotomicus* (= *Ips*) *latidens* (LeConte) (85 trees, 23.9%) and emarginate ips, *I. emarginatus* (LeConte) (3 trees, 0.8%) colonizing *P. ponderosa* and *P. jeffreyi*. Few meaningful differences in levels of indirect tree mortality attributed to bark beetle attack were observed between early and late season burns. The incidence of root and root collar pathogens (*Leptographium* and *Sporothrix* spp.), including species known to be vectored by bark beetles, was low (18% of trees sampled). The implications of these and other results to management of *P. ponderosa* and *P. jeffreyi* forests are discussed in detail.

© 2010 Published by Elsevier B.V.

1. Introduction

Many fire-adapted forest ecosystems in the western USA are denser and more spatially homogenous, have more small trees and fewer large trees, and have much higher fuel loads than prior to Euro-American settlement. Such conditions are prevalent nationally, but most notable at lower elevations in the western USA where short-interval, low-moderate intensity fire regimes pre-

dominate (e.g., Kilgore and Taylor, 1979; Arno, 1980; Swetnam, 1990; Agee, 1993; Covington and Moore, 1994; Skinner and Chang, 1996; Taylor and Skinner, 1998; Taylor, 2000; Swetnam and Baisan, 2002; Stephens et al., 2003). In general, these forests are characterized by the presence of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., an integral component of three cover types and a major component of >65% of all forests in the western USA (Burns and Honkala, 1990). In California, USA, highly effective fire suppression and differential cuttings of large-diameter, fire-tolerant tree species, such as *P. ponderosa* and Jeffrey pine, *P. jeffreyi* Grev. and Balf., have resulted in substantial changes in the structure and composition of interior *P. ponderosa* forests. Open park-like forests of widely dispersed *P. ponderosa* and *P. jeffreyi* were once common, particularly on xeric sites (Oliver, 2000). Frequent thinning

[☆] This article was written and prepared by U.S. Government employees on official time and it is, therefore, in the public domain and not subject to copyright.

* Corresponding author. Tel.: +1 530 759 1708; fax: +1 530 747 0241.

E-mail address: cfettig@fs.fed.us (C.J. Fettig).

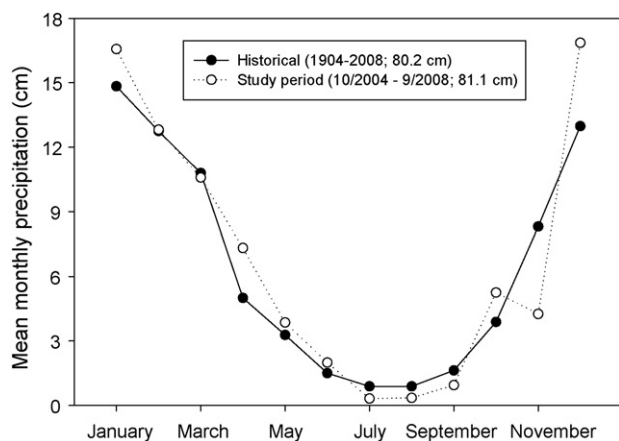


Fig. 1. Historical and 2004–2008 mean monthly precipitation at Truckee, California, USA (~15 km SSW of study site).

of small-diameter trees and fire-intolerant tree species by low-intensity surface fires, and competitive exclusion of tree seedlings by understory grasses, are believed to have maintained such conditions (Oliver, 2000).

In recent yr, large and severe wildfires have heightened public concern in the western USA. Currently, >10 million ha of forests are classified as having moderate to high fire hazards (Stephens and Ruth, 2005) and fuel reduction treatments have been widely promoted to reduce future wildfire impacts. Prescribed fire is now commonly used to reduce the buildup of hazardous fuels and to restore fire-adapted forest ecosystems (Agee and Skinner, 2005). Generally, prescribed burns are effective at reducing fire hazard (Pollet and Omi, 2002) particularly when canopy bulk density is low enough so that active crown fire spread is unlikely (Fulé et al., 2002; Agee and Skinner, 2005), as is typical of some *P. ponderosa* and *P. jeffreyi* forests. Mechanical fuel treatments (e.g., thinning from below) are also used, but have functionally different effects from prescribed burns on the fuel matrix and load within each fuel component.

In the Sierra Nevada of California, USA, high surface fuel moistures occur during late spring after snow melt or following the first rains or snow in mid- to late fall (Fig. 1). Historically, wildfires occurred most frequently in the late summer and early fall (van Wagendonk, 1972; Kilgore, 1973) during periods of peak lightning ignitions and lowest fuel moistures. Accordingly, late season (fall) prescribed burns are thought to more closely mimic natural patterns and processes, and therefore have often been favored by forest managers. The onset of fall precipitation also reduces the chance of fire escapes. However, late season burns coincide with stable atmospheric conditions when smoke dispersal is poor, and when forest managers face substantial restrictions on when burns may be implemented due to air quality concerns (Cahill et al., 1996). Furthermore, in fall it is possible to go directly from conditions too hot and dry to conduct prescribed burns to substantial snow cover, which effectively eliminates the fall burn window.

In order to meet their burn goals (e.g., acreage targets), forest managers are increasingly conducting burns during the early season (spring) when atmospheric conditions may be more favorable. Early season burns generally allow for conducting treatments when suitable fuel moistures are more consistent (i.e., little precipitation occurs during this time of yr in the Sierra Nevada), and are not reliant on recent or impending precipitation, as is the case in fall. However, forest managers are concerned about potential increases in the amount of tree mortality, both direct tree mortality attributed to prescribed fire effects and indirect tree mortality attributed to bark beetle (Coleoptera: Curculionidae, Scolytinae) attack, during

and immediately following early season burns. Early season burns occur at the beginning of the annual growth period when plants are most susceptible to heat damage and when carbohydrate reserves are at their lowest levels (Hough, 1968). Furthermore, it has been reported that burns implemented during the growing season result in greater amounts of tree mortality than those implemented during the dormant season, and may also cause increased amounts of fine root damage (Swezy and Agee, 1991). On the other hand, late season burns are likely to be of greater intensity (Skinner and Chang, 1996), and have been reported to result in greater amounts of tree mortality than early season burns (Thies et al., 2005). Schwilk et al. (2006) reported levels of tree mortality were related to fire intensity rather than differences in tree phenology in Sequoia National Park, USA.

Levels of tree mortality following prescribed burns depend on numerous factors including, but not limited to, tree species, tree size, phenology (season or life history stage), degree of fire-caused injuries, initial and post-fire levels of tree vigor, the post-fire environment, and the frequency and severity of other predisposing, inciting and contributing factors (Knapp et al., 2009). Prescribed burns may influence the amount of bark beetle-caused tree mortality by affecting the vigor of residual trees; the size, distribution and abundance of preferred hosts; and the physical environment within forest stands (Parker et al., 2006; Fettig et al., 2007). Volatiles released from fire-injured trees include monoterpenes that are known to influence the physiology and behavior of tree-killing bark beetles (Seybold et al., 2006). Early season burns stress trees just prior to the major flight activity periods of many bark beetles (Fettig et al., 2004b, 2005). McHugh et al. (2003) examined the response of several bark beetle species to a spring wildfire, summer wildfire and fall prescribed fire in Arizona, USA. The percentage of trees attacked by *Dendroctonus* and *Ips* species was lowest following the fall burn (11% of total trees), intermediate following the summer wildfire (19%) and highest after the spring wildfire (41%). Schwilk et al. (2006) found the probability of bark beetle attack (several species) on pines did not differ between early and late season burns while the probability of attack on firs, *Abies* spp., was greater following early season burns.

The propensity for bark beetles to attack fire-injured trees has led to questions regarding how the amount and distribution of bark beetle-caused tree mortality affect efforts to restore fire-adapted forest ecosystems with prescribed fire (Parker et al., 2006). Concerns exist about the potential for bark beetle populations to increase in fire-injured trees and then colonize apparently healthy trees in adjacent areas (Rasmussen et al., 1996). Furthermore, little is known about the effects of prescribed fire on root and/or root collar fungal infections (e.g., from *Leptographium* spp.) that may be introduced by attacks from certain bark beetles, such as red turpentine beetle (RTB), *D. valens* LeConte. The primary objectives of this 3-yr study were to determine the effect of prescribed burn season on levels of tree mortality, levels of tree mortality attributed to prescribed fire effects (direct mortality), and levels of tree mortality attributed to bark beetle attack (indirect mortality) in *P. ponderosa* and *P. jeffreyi* forests. A secondary objective was to determine the incidence of root and root collar pathogens following the application of prescribed fire.

2. Materials and methods

2.1. Study site and associated conditions

This study was conducted on the Truckee Ranger District, Tahoe National Forest, California (39.45°N, 120.12°W; 1828 m mean elevation) during 2004–2008. The climate is characterized by warm, dry summers and cold, moist winters. Mean annual temperature is

Table 1

Pre-treatment (2004) and post-treatment (2008) stand conditions within 4-ha experimental plots on the Tahoe National Forest, California, USA.

Treatment	Slope (%)	Aspect (°)	Crown cover (%)	QMD (cm) ^a	SDI ^a	Trees (/ha)	Basal area (m ² /ha)	<i>P. ponderosa</i> (%) ^b	<i>P. jeffreyi</i> (%) ^b
A. 2004									
Untreated control	5.4 ± 0.7	308.9 ± 26.5	37 ± 4	34.0 ± 4.0	139.9 ± 34.9	247.1 ± 87.4	19.1 ± 4.2	83.3 ± 5.1	16.7 ± 5.1
Early season	8.3 ± 2.7	248.6 ± 20.8	41 ± 5	31.2 ± 2.6	173.8 ± 11.3	323.7 ± 61.4	23.5 ± 0.8	67.7 ± 17.3	32.3 ± 17.3
Late season	7.5 ± 2.1	224.6 ± 7.5	29 ± 4	37.3 ± 0.7	84.0 ± 8.3	111.2 ± 7.9	12.3 ± 1.3	56.7 ± 8.8	43.3 ± 8.8
B. 2008									
Untreated control	– ^c	–	–	34.0 ± 4.0	139.8 ± 34.8	246.4 ± 86.9	19.1 ± 4.2	83.3 ± 5.1	16.7 ± 5.1
Early season	–	–	–	32.5 ± 2.2	160.5 ± 10.0	275.6 ± 45.3	22.1 ± 0.8	67.1 ± 17.5	32.9 ± 17.5
Late season	–	–	–	40.1 ± 0.8	78.6 ± 8.0	92.7 ± 6.3	11.8 ± 1.3	59.8 ± 10.6	40.2 ± 10.6

Values are means ± SEM. No significant differences were observed among means in any column/yr ($df = 2, 6$; $P > 0.055$, all cases).^a QMD, quadratic mean diameter; SDI, stand density index.^b Based on numbers of trees.^c Unchanged.

~6.3 °C. Mean annual precipitation is ~80 cm [Fig. 1; at 39.22°N, 120.18°W; 1829 m elevation; Western Regional Climate Center] with most coming as snow between December and April. Stands were mechanically thinned from below in 1997 and 1998 leaving the residual stands relatively open and dominated by *P. ponderosa* and *P. jeffreyi* (Table 1), but a few (<1 tree/ha) incense cedar, *Calocedrus decurrens* (Torr.) Florin, white fir, *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr., and lodgepole pine, *P. contorta* Dougl. ex Loud., were also present. Few activity fuels (logging residues) were evident as a result of the earlier thinning operation. At the beginning of this study, mean stand density was 12.3 and 23.5 m²/ha and 111.2 and 323.7 trees/ha for late and early season burns, respectively. Mean crown cover ranged from 29 to 41% (Table 1).

One of the best-recognized inciting factors in tree and forest health decline is deficiency in moisture availability, which affects host tree vigor and thus defensive mechanisms, and the fitness and survivorship of insect herbivores such as bark beetles (Fettig et al., 2007). During the course of this study, precipitation was normal (Fig. 1). Much of northern California emerged from 4 yr of drought conditions with above normal precipitation in 2005. Mountain pine beetle (MPB), *D. ponderosae* Hopkins, and western pine beetle (WPB), *D. brevicornis* LeConte, activity declined accordingly, and Jeffrey pine beetle (JPB), *D. jeffreyi* Hopkins, activity was low at that time (USDA Forest Service, 2006). Drought conditions returned to northern California in 2007 and continued into 2008. Generally, MPB and WPB activity in the Sierra Nevada remained low to moderate during the latter 2 yr of this study (USDA Forest Service, 2008).

2.2. Treatments

In 2004, nine 4-ha square plots were established in stands of similar topography and structure. Adjacent plots were separated by >50 m. Fire lines consisting of several meter wide strips of exposed mineral soil were established around the perimeter of all plots. Treatments were randomly assigned to each plot ($n = 3$) and included: (1) untreated control (no manipulation), (2) early season prescribed burn, and (3) late season prescribed burn. Early season burns were applied on 25 May 2005 (plots 1 and 4) and 30 May 2005 (plot 9), and late season burns were applied 19–20 October 2005 (plots 2, 3 and 7). All prescribed burns were implemented by personnel of the Truckee and Sierraville Ranger Districts, Tahoe National Forest (USDA Forest Service) working in close consultation with our research team. In brief, prescribed burns were ignited by drip torch along one edge of each plot and generally allowed to burn without intervention to the opposite edge. On occasion, small burns were ignited around the base of larger trees prior to igniting the plot. Climatic conditions, fuels and other burn parameters are reported in Table 2.

2.3. Data collection

Pre-treatment data were obtained for each plot within five 0.081-ha circular subplots ($N = 45$) by conventional means: (1) number of trees (>8.9 cm dbh), (2) diameter at breast height (dbh, 1.37 m in height), (3) basal area, (4) tree species, (5) percent crown cover (by densitometer), (6) slope and (7) aspect. Subplots were permanently established with rebar. Ten 1-m² subplots ($N = 60$) were established in each burn plot with two associated with each 0.081-ha subplot (i.e., systematically placed 20.2 m from the center point) and divided into four equal (0.25 m²) quadrants. Two quadrants were destructively sampled before and two after burns were implemented. All litter, duff, and other small surface fuels (<2.54 cm diameter, 1- and 10-h fuels; cones excluded) were collected within 11 d of each burn, dried at 90 °C for 48 h, and weighed. Fuel consumption was calculated by subtracting the oven-dried weights of materials in post-burn quadrants from those of the pre-burn quadrants. Prior to burns, 10 high-registering thermometers were buried horizontally along the interface between the mineral soil and overlying organic layers in each burn plot ($N = 60$) to provide an estimate of peak soil temperatures. One thermometer was placed 1 m north of the center point of each 1-m² subplot. Thermometers were retrieved and temperatures recorded within 48 h of each burn.

Large downed woody fuels (≥ 100 h) were also sampled in association with each 0.081-ha subplot. A single transect 20.2 m in length was run in a northerly direction starting at each subplot center. This served as one side of a 20.2 by 4 m strip plot from within which downed woody fuels were sampled. Only fuels with a total length >0.5 m with large end diameter >5.0 cm were measured. For each qualifying log, the smallest and largest diameter within the strip plot, and total length within the strip plot to a minimum diameter of 2.54 cm were recorded. Mass was calculated using equations provided by Brown (1974, p. 18) incorporating specific gravity values obtained from van Wagendonk et al. (1996) for *P. ponderosa* and *P. jeffreyi* in the Sierra Nevada. Fuel consumption was calculated by subtracting post-burn from pre-burn estimates. Sampling was completed within 18 d of each burn.

In order to quantify fire severity, minimum and maximum heights of bole char and percent crown damage were recorded for all trees within each 0.081-ha subplot. Percent crown damage was determined by dividing length of crown scorch plus consumption by pre-burn total crown length. All heights were measured using a clinometer. Bole injury was further assessed on all trees within these subplots by visually dividing the tree bole into four quadrants based on cardinal directions. The cambium was sampled in the center of each quadrant to obtain a cambium kill rating (CKR) for each tree by methods similar to Hood et al. (2007). This was accomplished by drilling through the bark to the sapwood near

Table 2
Weather conditions, fuels and measures of fire intensity and fire severity following early and late season prescribed burns applied to 4-ha experimental plots on the Tahoe National Forest, California, USA, 2005.

Burn season	Wind speed (kph) ^a	Soil interface temperature (°C) ^{b,c}	Fuels (≤10 h, T/ha) ^{a,b,d}	Fuel consumption (≤10 h, %) ^{b,d}	Fuels (≥100 h, T/ha) ^{a,b,d}	Fuel consumption (≥100 h, %) ^{b,d}	Crown damage (%) ^b	Average bole char height (m) ^b	CKR ^{b,e}
Early	3.2 ± 0.9	81.0 ± 22.0 a	49.4 ± 3.6 b	38.1 ± 8.6 a	18.8 ± 5.1 b	53.9 ± 5.6 a	40.8 ± 3.1 a	1.4 ± 0.2 a	0.3 ± 0.1 a
Late	2.4 ± 0.3	88.1 ± 1.3 a	29.1 ± 7.9 a	42.2 ± 0.6 a	3.1 ± 1.3 a	86.8 ± 4.9 b	17.4 ± 3.0 b	0.7 ± 0.1 b	1.1 ± 0.2 b

Values are means ± SEM.

^a Conditions at the field site immediately prior and during burns. Air temperature was 22.2 ± 0.3 and 10.4 ± 1.9 °C; relative (%) humidity was 36.4 ± 1.1 and 61.7 ± 6.5 for early and late season burns, respectively.

^b Means followed by the same letter within column are not significantly different ($P > 0.05$; $df = 1, 4$).

^c Ten high-registering thermometers were buried horizontally along the interface between the mineral soil and overlying organic layers.

^d Classes based on timelag principle (Pyne et al., 1996).

^e CKR, Cambium kill rating; values 0–4 based on the number of quadrants sampled per tree that contained dead cambium (Hood et al., 2007).

groundline with a 2.54 cm diameter bit. Each sample was then visually inspected in the field for color and condition of tissue. Dead cambium is darker in color, often resin soaked, and often hard in texture. Live cambium is lighter in color, moist and pliable. A rating of 0–4 was recorded for each tree by totaling the number of quadrants with dead cambium (Table 2).

A 100% cruise (census) was conducted on each experimental plot to locate dead and dying trees by presence of fading throughout the crown, an irreversible symptom of tree mortality. Surveys were first conducted in May 2005 (i.e., just prior to application of early season burns) to capture any recent tree mortality that occurred external to the study period. These trees were excluded from our analyses. Subsequent surveys were conducted in July 2005, May 2006, and October 2006–2008. In all cases, all recently killed trees >10.2 cm dbh were identified, tallied and causal agent of mortality identified. Tree species, dbh, crown color, colonizing bark beetle species, presence of wood borers (Coleoptera: Cerambycidae, Buprestidae), minimum and maximum heights of bole char, % crown damage, and number of RTB attacks [pitch tubes with oxidized phloem material (i.e., reddish-colored) present or granular boring dust] were recorded. A section of bark ~625 cm² was removed with a hatchet at ~2 m in height on at least two aspects to determine if any bark beetle galleries were present in the phloem or cambium. The shape, distribution and orientation of galleries, and host tree species are commonly used to distinguish among bark beetle species (Furniss and Carolin, 1977). In some cases, deceased bark beetles were present beneath the bark to supplement identifications based on gallery formation. In addition, surveys of all live trees were conducted 1 yr after the application of early and late season burns for RTB attacks.

During summer 2006, lateral roots were sampled from one randomly selected 0.081-ha subplot within each experimental plot. Within the subplot, two woody lateral roots (non-decaying) were excavated from each of five selected codominant trees each representing CKR 0 through 4 (Hood et al., 2007). Excavated roots remained attached, but were exposed to a distance of ~0.5–0.75 m from the bole. 6–10 cores were extracted from the root collar along the length of exposed root to a depth of 1–2 cm using a 4 mm diameter increment hammer (Otrosina et al., 1999, 2002). Extracted cores were immediately placed in an ice chest and transported to the laboratory for plating onto cycloheximide amended 1.25% malt extract agar using methods previously described (Otrosina et al., 1999). Plates were observed daily for fungal growth and Ophiostomatoid fungi developing were recorded and subcultured on unamended 1.25% malt broth agar and identified by colony and microscopic morphology.

2.4. Analyses

Primary variables of interest were the mean percentage of trees killed by (1) all causes (total mortality), (2) prescribed fire (direct mortality), and (3) bark beetle species (indirect mortality) by 10.2-cm diameter classes [10.2–20.2 cm (15.2 cm midpoint), 20.3–30.4 cm (25.4 cm), 30.5–40.5 cm (35.6 cm), 40.6–50.7 cm (45.7 cm), >50.7 cm, ≥10.2 cm (all trees); dbh]. Mortality was only attributed to bark beetles when burn severity rankings on individual trees were ≤3 (Fettig et al., 2008, 2010). A ranking of four indicates the tree was directly killed by prescribed fire, regardless of any evidence of bark beetle attack, as indicated by external measures of fire severity (i.e., charring of bark plates and fissures with substantial bark consumption). Therefore, a distinction is made between trees directly killed by prescribed fire and those predisposed by fire to bark beetle attack (Ganz et al., 2003).

The experimental design was completely randomized with three treatments and three replicates per treatment ($df = 2, 6$). A

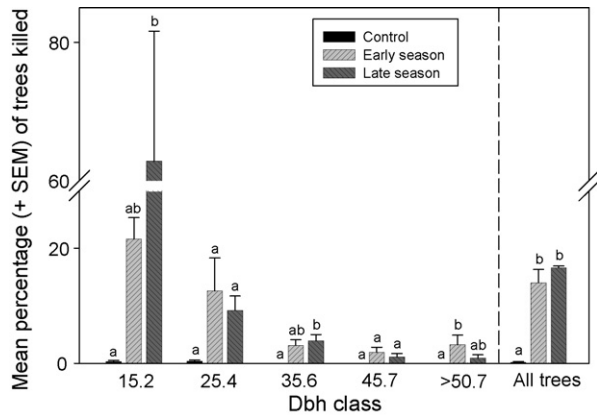


Fig. 2. Mean percentage of trees killed (all sources combined) by diameter class (mid-point of 10-cm diameter classes shown except for largest diameter class) 3 yr after prescribed burns were implemented, Tahoe National Forest, California, USA. Means (+SEM) followed by the same letter within groups are not significantly different (Tukey's HSD, $P > 0.05$).

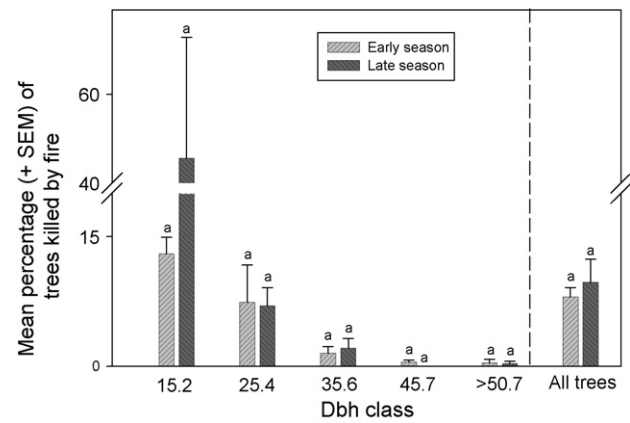


Fig. 3. Mean percentage of trees killed by prescribed burns (direct mortality) by diameter class (mid-point of 10-cm diameter classes shown except for largest diameter class) 3 yr after prescribed burns were implemented, Tahoe National Forest, California, USA. Means (+SEM) followed by the same letter within groups are not significantly different ($P > 0.05$).

test of normality was performed and appropriate transformations were used when data deviated significantly from a normal distribution. We performed an analysis of variance on each response variable at $\alpha = 0.05$ (SAS Institute Inc., Cary, NC, USA). If a significant treatment effect was detected, Tukey's multiple comparison test (Tukey's HSD) was used for separation of treatment means requiring more than one comparison.

3. Results and discussion

3.1. Overall tree mortality

A total of 816 trees (9.9% of all trees) died during this 3-yr study, of which 71.6% (584 trees), 27.5% (224 trees) and 0.9% (8 trees) occurred on early season, late season and untreated control plots, respectively. These values represent mortality attributed to all sources (i.e., prescribed fire, bark beetles, pathogens and unidentified sources, and their many interactions). Significantly higher levels of tree mortality occurred following early and late season burns compared to the untreated control (all trees; $F_{2,6} = 42.4$, $P < 0.001$), however no significant difference was observed between burn treatments (Fig. 2). For the largest trees (>50.7 cm dbh), significantly higher levels of tree mortality occurred on early season burns than the untreated control ($F_{2,6} = 5.5$; $P = 0.044$), but for the smallest trees (15.2 cm dbh class) mortality was significantly higher on late season burns compared to the control ($F_{2,6} = 8.3$; $P = 0.019$) (Fig. 2). For trees in the middle diameter classes, we only observed a significant treatment effect in the 35.6 cm dbh class in which higher levels of tree mortality occurred on late season burns compared to the untreated control ($F_{2,6} = 5.8$, $P = 0.040$). No significant differences were observed between early and late season burns within

any dbh class (Fig. 2). Overall, tree mortality was concentrated in the smallest dbh class for both early ($F_{4,10} = 7.0$, $P = 0.005$) and late season burns ($F_{4,10} = 9.8$, $P = 0.002$) (Table 3).

As a result of tree mortality, quadratic mean diameter increased while stand density index (SDI), trees/ha, and basal area declined for both early and late season burns, however no significant differences were observed among treatment means ($P > 0.12$, all cases). Effects were generally more pronounced for late season burns (Table 1). Slight shifts in tree species composition were observed for both early and late season burns, but not for the untreated control where tree mortality was negligible (Fig. 2).

3.2. Direct tree mortality

The majority (56.5%, 461 trees) of tree deaths was attributed to direct mortality resulting from prescribed burns, and was highly concentrated in the smallest dbh class (84.8% of all direct mortality; Fig. 3). Generally, larger trees are more fire-resistant (Peterson and Ryan, 1986; Harrington, 1993; Agee and Skinner, 2005; Thies et al., 2005; Sieg et al., 2006), particularly those species that have thick bark (Ryan and Reinhardt, 1988), which reduces cambium injury (Martin, 1963; Hood et al., 2008). Furthermore, larger trees tend to have higher crowns (i.e., heights to the base of the live crown) and greater heat sink capacities resulting in less fire-related injury (Ryan and Reinhardt, 1988). Regelbrugge and Conard (1993) reported decreased probability of post-fire mortality in *P. ponderosa* with increasing tree diameter and height in the central Sierra Nevada. However, Hood et al. (2008) found the predicted probability of dead cambium in *P. ponderosa* increased as diameter increased, but the relationship was reversed for all other tree species sampled in their study. Other authors have suggested that

Table 3

Mean percentage ($\pm$ SEM) of trees killed by all causes (total mortality), prescribed fire (direct mortality) and bark beetles (all bark beetle species combined; indirect mortality) among diameter classes (mid-point of 10-cm diameter classes shown except for largest diameter class) 3 yr after early and late season prescribed burns were implemented on the Tahoe National Forest, California, USA.

Dbh class	Total mortality		Direct mortality		Indirect mortality	
	Early season	Late season	Early season	Late season	Early season	Late season
15.2	21.6 $\pm$ 3.7 a	62.8 $\pm$ 18.8 a	13.0 $\pm$ 1.9 a	45.6 $\pm$ 27.2 a	8.7 $\pm$ 2.1 a	19.7 $\pm$ 7.0 a
25.4	12.6 $\pm$ 5.7 ab	9.2 $\pm$ 2.5 b	7.4 $\pm$ 4.3 ab	7.0 $\pm$ 2.1 a	5.2 $\pm$ 1.7 ab	2.2 $\pm$ 0.9 b
35.6	3.1 $\pm$ 1.0 b	3.9 $\pm$ 1.1 b	1.5 $\pm$ 0.8 b	2.1 $\pm$ 1.1 a	1.6 $\pm$ 0.4 b	1.8 $\pm$ 0.1 b
45.7	1.9 $\pm$ 1.0 b	1.1 $\pm$ 0.6 b	0.5 $\pm$ 0.2 b	0.0 $\pm$ 0.0 a	1.4 $\pm$ 0.8 b	1.1 $\pm$ 0.6 b
>50.7	3.2 $\pm$ 1.7 b	0.9 $\pm$ 0.6 b	0.4 $\pm$ 0.4 b	0.3 $\pm$ 0.3 a	2.8 $\pm$ 1.3 ab	0.7 $\pm$ 0.7 b

Means ($\pm$ SEM) followed by the same letter within columns are not significantly different (Tukey's HSD, $P > 0.05$).

older *P. ponderosa* are more susceptible to mortality after fire than younger, mature trees (Kolb et al., 2007). Larger trees are more likely to die than smaller trees with similar levels of crown and cambium injury (Hood et al., 2007), perhaps because of greater basal duff accumulations resulting in increased fire duration and intensity, elevated levels of fine root injury, and reduced tree vigor, especially during periods of drought. In Arizona, McHugh and Kolb (2003) reported mortality 3 yr after fire was highest for trees with the smallest diameters (<20 cm dbh), which agrees with our study. Mortality decreased as diameter increased between 20 and 50 cm dbh as would be expected due to increasing bark thickness. However, mortality increased as diameter increased among the largest trees (>50 cm dbh) in their study. Similarly, Fulé et al. (2002) reported 67% of large-diameter (>50 cm dbh) *P. ponderosa* died within 2 yr following prescribed burns compared with 19% mortality for smaller diameter trees. Other studies have reported similar trends described as a “U-shaped” distribution of *P. ponderosa* mortality by tree diameter (Kolb et al., 2007), which is not consistent with our study (Figs. 2 and 3) and others conducted in northern California (Schwilke et al., 2006; Fettig et al., 2008, 2010). Direct tree mortality was concentrated in the smallest dbh class for early season burns ($F_{4,10} = 6.7$, $P = 0.007$), but no significant differences were observed for late season burns ($F_{4,10} = 2.6$, $P = 0.105$) (Table 3), due to high levels of variation in the 15.2 cm dbh class.

We observed no significant differences in the amount of direct mortality between early and late season burns (all trees; $F_{1,4} = 0.3$, $P = 0.588$) or within individual dbh classes ($P > 0.12$, all cases; Fig. 3). Late season burns are generally thought to be of greater intensity (Ryan et al., 1988; Skinner and Chang, 1996; Thies et al., 2005), and therefore presumably result in higher levels of tree mortality, particularly in smaller diameter classes. Our late season burns were implemented during cooler (~10 and 22 °C) and moister (~62 and 36% relative humidity) weather conditions than early season burns, but resulted in significantly higher levels of large (≥ 100 -h) downed woody fuel consumption and CKR (Table 2). Greater crown damage and bole char heights were observed following early season burns (Table 2), which may be influenced by pre-treatment stand density (Table 1). Substantial fuel consumption occurred following both early and late season burns (Table 2), and overall surface fuel loads were moderate (~39 t/ha, ≤ 10 -h) for *P. ponderosa* and *P. jeffreyi* forests (Stephens, 2004). Mean maximum soil temperatures were ~81 and 88 °C for early and late season burns, respectively (Table 2). A temperature of 60 °C for 1 min is considered lethal to plant tissues (Hare, 1961), and it is therefore likely that heat injury occurred to some fine roots perhaps weakening trees and rendering them more susceptible to bark beetle attacks and/or fungal infections. Heating also caused significantly more cambium injury (CKR) in late season burns compared to early season burns, although injury was low for both treatments (Table 2).

Trees that died directly from prescribed burns had significantly higher levels of crown damage compared to all other trees following early season ($F_{2,6} = 63.5$, $P < 0.001$; 80.6 ± 3.1 versus $40.8 \pm 3.1\%$; mean $\pm$ SEM) and late season burns ($F_{2,6} = 9.4$, $P = 0.014$; 51.9 ± 12.0 versus $17.4 \pm 3.0\%$). However, no significant differences were observed for average bole char height between trees that died directly from prescribed burns and all other trees ($P > 0.14$, both cases). There were no significant differences between early and late season burns in crown damage or average bole char height on trees that died from direct fire effects ($P > 0.08$, both cases). Most researchers that have examined the effect of fire on mortality of conifers in the western USA have concluded that crown injury is the most important predictive variable (Fowler and Sieg, 2004). Recent work on *P. ponderosa* and *P. jeffreyi* in California found crown injury, cambium injury (CKR), dbh and presence of RTB attacks were important predictors of post-fire survivability (Hood et al., 2007).

3.3. Indirect tree mortality

Following prescribed fire, tree mortality may be immediate due to consumption of living tissue or heating of critical plant tissues, or can be delayed, occurring over the course of a few yr, as a result of fire injuries to the crown, bole or roots (Hood et al., 2007). In addition to direct mortality attributed to fire effects, bark beetles may attack and kill trees that were injured by fire, but that otherwise likely would have survived (Parker et al., 2006). Furthermore, these brood trees (i.e., those containing immature stages of bark beetles and attacking adults) may serve as a source of beetles and attractive semiochemicals (i.e., kairomones and pheromones) that attract other beetles into the vicinity resulting in additional levels of subsequent tree mortality (e.g., group kills resulting from WPB attacks were observed following spring burns). During our study, MPB (56 trees) and WPB (67 trees) were found colonizing *P. ponderosa*; and JPB was found colonizing *P. jeffreyi* (seven trees). We also found pine engraver (PE), *Ips pini* (Say) (137 trees), and, to a much lesser extent, *Orthotomicus* (= *Ips*) *latidens* (LeConte) (85 trees) and emarginate ips, *I. emarginatus* (LeConte) (three trees) colonizing *P. ponderosa* and *P. jeffreyi*.

Some wood borers are attracted to fire (Evans, 1966), smoke (Wickman, 1964) and fire-injured trees (Rasmussen et al., 1996), but their contribution to tree mortality is largely unknown following mixed-severity wildfire (Rasmussen et al., 1996) or prescribed fire (Fettig et al., 2008). Some wood borers are regarded as forest pests. For example, California flatheaded borer, *Melanophila californica* Van Dyke, is known to cause tree mortality, particularly during extended periods of drought (Furniss and Carolin, 1977). McHugh et al. (2003) found wood borers were the most common insect found in trees following mixed-severity wildfires and prescribed fire in *P. ponderosa* forests in Arizona. Fettig et al. (2008) reported that wood borer attacks directly contributed to tree mortality [i.e., based on timing (yr) of crown fade following prescribed fire and absence of attacks by tree-killing bark beetles] in numerous fire-injured trees 2 yr after the application of prescribed fires in the northern Sierra Nevada, and that in the absence of such attacks tree mortality would likely not have occurred. However, evidence of such an effect was not observed in a second study conducted in the Southern Cascades of California (Fettig et al., 2010) or in this study.

The precise role of each bark beetle species in causing tree mortality on our experimental plots is uncertain. Fire-injured *P. ponderosa*, and to a lesser extent *P. jeffreyi*, are susceptible to colonization by several species of bark beetles. For example, Fettig et al. (2008) reported the application of prescribed fire resulted in significant increases in bark beetle-caused tree mortality (all species) and for WPB, MPB and engraver beetles (*Ips* spp.) individually in *P. ponderosa* forests in the northern Sierra Nevada. In our study, attacks by several bark beetle species were accompanied by those of other bark beetles within the same tree. Accordingly, in reference to WPB, MPB, and JPB, we attributed tree mortality to one of these species if evidence of colonization was found despite the potential existence of other bark beetle species. On occasion (14 trees), we found PE and *O.* (= *Ips*) *latidens* infesting the same tree and in these situations we attributed tree mortality to PE. Tree mortality was attributed to *Ips* spp. (including PE) only when evidence of WPB, MPB, or JPB colonization was absent. It is possible that bark beetles attacked the upper bole of trees above our sampling height that we therefore classified as dead due to prescribed fire effects on burned plots (Breece et al., 2008). On the other hand, *Ips* spp. are known to attack dying trees (i.e., they do not require succulent phloem to reproduce) and therefore it is possible that some mortality attributed to *Ips* attacks could have occurred in absence of these attacks.

We also found RTB colonizing many trees, both live and dead. Red turpentine beetle attacks are usually confined to basal portions

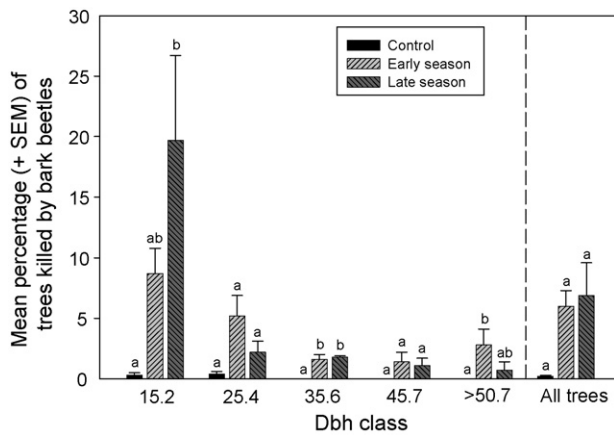


Fig. 4. Mean percentage of trees killed by bark beetles (all bark beetle species combined; indirect mortality) by diameter class (mid-point of 10-cm diameter classes shown except for largest diameter class) 3 yr after prescribed burns were implemented, Tahoe National Forest, California, USA. Means (+SEM) followed by the same letter within groups are not significantly different (Tukey's HSD, $P > 0.05$).

of previously stressed, weakened, or dead and dying trees (Furniss and Carolin, 1977), or those under attack by other bark beetles, such as WPB (Fettig et al., 2004a). Attacks typically do not cause tree mortality in the absence of confounding factors. However, tree mortality was attributed to RTB in a 17-yr-old *P. ponderosa* plantation in northern California (Rappaport et al., 2001), for several trees in stands where logging residues were chipped and retained on-site in northern California (Fettig et al., 2006), and of *P. tabuliformis* Carriere in China where RTB was accidentally introduced (Li et al., 2001). Despite this, we did not attribute tree mortality to RTB attacks in this study.

A total of 355 trees (4.3% of all trees) were killed by bark beetles (all species) during this study. Overall, we observed no significant treatment effect in the amount of bark beetle-caused tree mortality (all trees; $F_{2,6} = 4.3$, $P = 0.070$) despite substantial differences in levels of bark beetle-caused tree mortality between burn treatments and the untreated control (Fig. 4). Indirect mortality attributed to bark beetle attack was concentrated in the smallest dbh class for late season ($F_{4,10} = 6.7$, $P = 0.007$) and early season burns ($F_{4,10} = 4.9$, $P = 0.019$) (Table 3), but for early season burns no significant difference was observed between the smallest and largest (>50.7 cm) dbh classes. For the largest trees (>50.7 cm dbh), significantly higher levels of indirect tree mortality occurred on early season burns than the untreated control ($F_{2,6} = 5.6$; $P = 0.043$), however, greater amounts of bark beetle-caused tree mortality occurred following late season burns in the smallest dbh class compared to the untreated control ($F_{2,6} = 5.4$; $P = 0.046$) (Fig. 4). For trees in the middle dbh classes, we only observed a significant treatment effect in the 35.6 cm dbh class in which higher levels of bark beetle-caused tree mortality occurred on both early and late season burns compared to the untreated control ($F_{2,6} = 20.9$; $P = 0.002$; Fig. 4). No bark beetle-caused tree mortality occurred in the untreated control in the three largest dbh classes (>30.5 cm dbh; Fig. 4). In all cases, no significant differences were observed between early and late season burns (Fig. 4).

Trees that died from indirect mortality attributed to bark beetle attack had significantly higher levels of crown damage compared to all others following early season ($F_{2,6} = 63.5$, $P < 0.001$; $80.0 \pm 1.3\%$ versus $40.8 \pm 3.1\%$) and late season burns ($F_{2,6} = 9.4$, $P = 0.014$; $59.9 \pm 3.1\%$ versus $17.4 \pm 3.0\%$). However, no significant differences were observed for average bole char heights ($P > 0.14$, both cases). There was no significant difference in average bole char height on trees that died from bark beetle attack between burn treatments ($F_{1,4} = 2.8$; $P = 0.169$), but significantly higher levels of crown dam-

age occurred on such trees following early season burns ($F_{1,4} = 35.5$, $P = 0.004$; $80.0 \pm 1.3\%$ versus $59.9 \pm 3.1\%$), which differs from trends observed for direct mortality. In this context, crown damage may serve as a surrogate indicator of tree stress (i.e., which increases the susceptibility of trees to bark beetle attack and thus indirect mortality) while bole char height serves as a surrogate indicator of cambium injury or death. In some cases (e.g., JPB, MPB and WPB), trees must have enough green phloem and live buds to permit new needle growth for bark beetle colonization and brood production to occur (Fischer, 1980). To that end, *P. ponderosa* and *P. jeffreyi* are capable of producing new needle growth after significant crown damage has occurred following heating, particularly in the lower crown, but that weakens tree defenses to bark beetle attack (Wallin et al., 2003). McHugh et al. (2003) showed the amount of crown damage and bark beetle attack (rated as none, partial, or mass attack) were important variables for predicting the mortality of *P. ponderosa* following fire. Siegel et al. (2006) quantified tree attributes, degree of tree injury, and insect presence from 5083 trees following mixed-severity wildfires in the western USA. They reported crown scorch (percentage) and consumption (percentage) volume collectively accounted for the majority of predictive capacity in their models to predict individual tree survival. The addition of dbh and presence of *Ips* beetles increased predictive power. Breece et al. (2008) concluded canopy damage from fire was a strong and consistent predictor of post-fire mortality of *P. ponderosa*, and that bark beetle attacks and bole char rating were less consistent predictors.

3.3.1. *Ips* spp.

As with direct mortality, the majority (82.0%) of bark beetle-caused tree mortality occurred in the smallest dbh class most of which was attributed to *Ips* spp. A total of 225 trees (2.7% of all trees) were killed by *Ips* spp. of which 95.6% occurred in the smallest dbh class. No *Ips*-caused tree mortality occurred in the 35.6 and >50.7 cm dbh classes (Fig. 5). Overall, we observed a significant treatment effect in the amount of *Ips*-caused tree mortality (all trees; $F_{2,6} = 5.3$, $P = 0.047$) and within the smallest dbh class ($F_{2,6} = 10.7$, $P = 0.010$) with significantly higher levels occurring on late season burns than the untreated control (Fig. 5). No other significant differences were observed (Fig. 5).

Ips spp. generally colonize slash, saplings and weakened trees or trees previously colonized by other bark beetle species (Kegley et al., 1997). Outbreaks are often short-lived, but increase in duration and extent when suitable host material is plentiful and populations

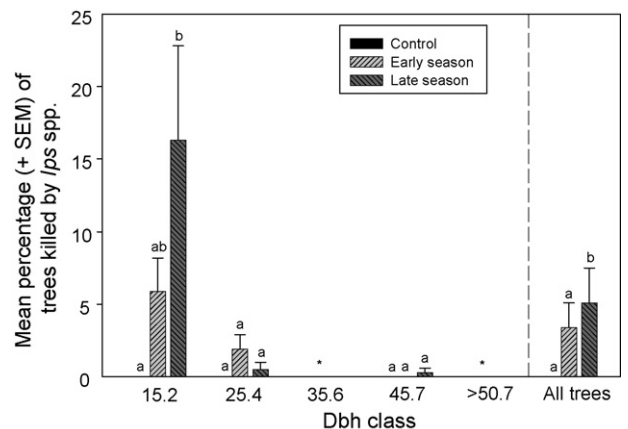


Fig. 5. Mean percentage of trees killed by *Ips* spp. by diameter class (mid-point of 10-cm diameter classes shown except for largest diameter class) 3 yr after prescribed burns were implemented, Tahoe National Forest, California, USA. Means (+SEM) followed by the same letter within groups are not significantly different (Tukey's HSD, $P > 0.05$). Asterisk denotes that no trees were attacked in that size class regardless of treatment.

grow sufficiently large to colonize apparently healthy trees. In our study, few larger trees (>20.3 cm dbh; 10 trees) were killed by *Ips* spp., but ~16% of all trees in the 15.2 cm dbh class died as a result of *Ips* attacks following late season burns. Ganz et al. (2003) studied the effects of prescribed fire on susceptibility of *P. ponderosa* and *P. jeffreyi* to bark beetle attack in two case studies in California, and reported >30% of pines were killed by PE the first yr following prescribed burns. Bradley and Tueller (2001) reported 36 of 389 pines were colonized by *Ips* spp. the yr following prescribed burns in the Lake Tahoe Basin of California and Nevada, USA. Furthermore, Fettig et al. (2008) reported the application of prescribed fire resulted in a significant increase in the proportion of pines (>19 cm dbh) killed by *Ips* spp. with ~99% of all *Ips*-caused tree mortality occurring on burned plots. Generally, *Ips* spp. colonize smaller trees (5–20 cm dbh; Kegley et al., 1997), and attack rates are negatively correlated with tree dbh in *P. ponderosa* (Kolb et al., 2006; Negrón et al., 2009). In some areas, top killing of live pines by *Ips* spp. is common, but was not evident in our study. Breece et al. (2008) reported attacks by *Ips* spp. were more common in the upper bole than the lower bole following fire and increased by 3.7× for every 2 m increase in height on the tree bole. In their study, most attacks also occurred in the smaller diameter classes.

3.3.2. Western pine beetle

A total of 67 *P. ponderosa* (0.8% of all trees) were killed by WPB. Western pine beetle is a major cause of *P. ponderosa* mortality in portions of the western USA (Miller and Keen, 1960). Under certain conditions, the beetle can attack and kill apparently healthy trees of all ages and size classes. *Pinus ponderosa* is the only host of WPB present in these stands (Miller and Keen, 1960). Overall, we observed a significant treatment effect in the amount of WPB-caused tree mortality (all trees; $F_{2,6} = 5.4$, $P = 0.045$) and within the smallest dbh class ($F_{2,6} = 28.1$, $P < 0.001$). In both cases, significantly more WPB-caused tree mortality occurred on early season burns than the untreated control (Fig. 6), the latter in which no WPB-caused tree mortality occurred. While large numbers of WPB adults are active throughout much of the yr, flight activity peaks in June in *P. ponderosa* and *P. jeffreyi* forests (Fettig et al., 2004b; data from site ~166 km NNW at similar elevation), which likely explains the effect observed. A similar effect was observed for WPB following chipping of *P. ponderosa* in spring compared with the late summer (Fettig et al., 2006; DeGomez et al., 2008), and was linked to high concentrations of attrac-

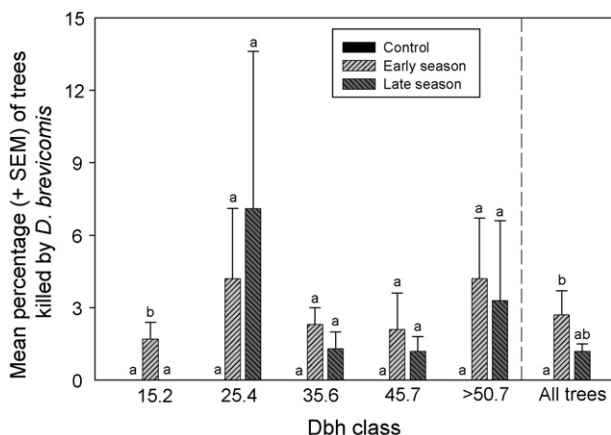


Fig. 6. Mean percentage of trees killed by western pine beetle, *Dendroctonus brevicornis* LeConte, by diameter class (mid-point of 10-cm diameter classes shown except for largest diameter class) 3 yr after prescribed burns were implemented, Tahoe National Forest, California, USA. Means (+SEM) followed by the same letter within groups are not significantly different (Tukey's HSD, $P > 0.05$).

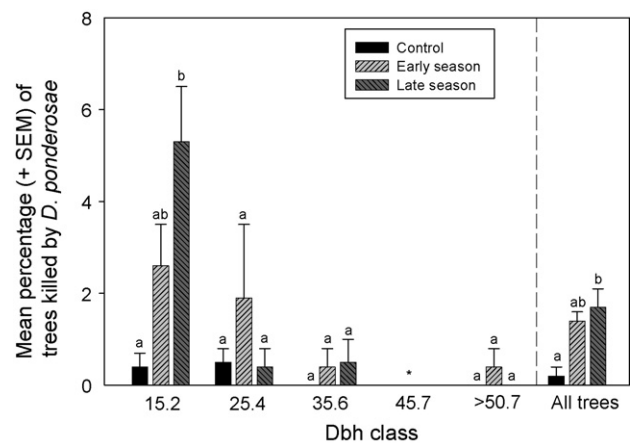


Fig. 7. Mean percentage of trees killed by mountain pine beetle, *Dendroctonus ponderosae* Hopkins, by diameter class (mid-point of 10-cm diameter classes shown except for largest diameter class) 3 yr after prescribed burns were implemented, Tahoe National Forest, California, USA. Means (+SEM) followed by the same letter within groups are not significantly different (Tukey's HSD, $P > 0.05$). Asterisk denotes that no trees were attacked in that size class regardless of treatment.

tive volatiles released from chips during the major flight activity period.

About 43% (29 trees) of all WPB-caused tree mortality occurred on early season burns within the smallest dbh class which is surprising given the beetle's preference for larger diameter trees (50.8–81.3 cm dbh; Person, 1928), but agrees with other studies that evaluated the effects of prescribed fire on levels of bark beetle-caused tree mortality in northern California (Fettig et al., 2008, 2010). No WPB-caused tree mortality occurred following late season burns in the smallest dbh class (Fig. 6). McHugh et al. (2003) reported that WPB colonized only three of 222 trees following a prescribed fire in Arizona. Similarly, Sánchez-Martínez and Wagner (2002) detected no significant difference in the amount of WPB-caused tree mortality between managed (including prescribed fire) and unmanaged stands in Arizona, but others have established a link between fire-injury and the increased susceptibility of *P. ponderosa* to WPB attack (e.g., Miller and Patterson, 1927; Fischer, 1980).

3.3.3. Mountain pine beetle

A total of 56 *P. ponderosa* (0.7% of all trees) were killed by MPB. Mountain pine beetle occurs throughout British Columbia, Alberta, most of the western USA, and into northern Mexico, and colonizes several pines, most notably *P. contorta*, *P. ponderosa*, sugar pine, *P. lambertiana* Dougl., whitebark pine, *P. albicaulis* Engelm., and western white pine, *P. monticola* Dougl. ex D. Don (Furniss and Carolin, 1977). The role of MPB in *P. ponderosa* stands in California is usually secondary to that of WPB (Miller and Keen, 1960), particularly in larger diameter trees.

Overall, we observed a significant treatment effect in the amount of MPB-caused tree mortality (all trees; $F_{2,6} = 6.7$, $P = 0.029$) and within the smallest dbh class ($F_{2,6} = 7.5$, $P = 0.023$). In both cases, significantly more MPB-caused tree mortality occurred on late season burns than the untreated control (Fig. 7), which is different than the effect we observed for WPB. While large numbers of MPB are flight active throughout much of the yr, flight activity generally peaks in late summer and fall (August and October) in *P. ponderosa* and *P. jeffreyi* forests (Fettig et al., 2004b), which likely explains the effect observed. No MPB-caused tree mortality occurred in the untreated control within the three largest dbh classes (>30.5 cm), and none occurred in the 45.7 cm dbh class within any treatment (Fig. 7). Fettig et al. (2008) reported the application of prescribed fire resulted in significant increases in MPB-caused tree mortality

except within the two largest dbh classes (>49.6 cm dbh). In their study, ~83% of all MPB-caused tree mortality occurred on burned plots. Fettig et al. (2010) reported similar results in the Southern Cascades where the amount of MPB-caused tree mortality was significantly greater following prescribed burns in the two smallest dbh classes (<39.3 cm dbh). Alternatively, others have found no effect (Rasmussen et al., 1996; McHugh et al., 2003; Elkin and Reid, 2004), particularly in *P. contorta*.

3.3.4. Jeffrey pine beetle

Few *P. jeffreyi* (seven trees) were colonized by JPB and therefore statistical analyses were not conducted. All JPB-caused tree mortality occurred on early (four trees) or late season burns. Jeffrey pine beetle can be a significant cause of *P. jeffreyi* mortality in portions of the Sierra Nevada (Furniss and Carolin, 1977), but several authors have reported few trees being colonized by JPB following burns (Bradley and Tueller, 2001; Ganz et al., 2003; Fettig et al., 2008). Maloney et al. (2008) found significant *P. jeffreyi* mortality following prescribed burns in mixed-conifer forests, but reported that JPB attacks occurred on only 11% of trees that died. While *P. jeffreyi* is moderately resistant to fire and shares many of the same adaptations to fire as *P. ponderosa*, it generally suffers less bark beetle-caused mortality following prescribed burns (Fettig et al., 2008). This may have more to do with the life history traits of JPB than any appreciable difference in the susceptibility of *P. ponderosa* and *P. jeffreyi* to bark beetle attack following similar levels of fire-injury. For example, JPB is univoltine and typically present in relatively low densities primarily breeding in slow growing trees of reduced vigor (Smith et al., 2009). Furthermore, a much larger complex of tree-killing bark beetles colonizes *P. ponderosa* than *P. jeffreyi* (Furniss and Carolin, 1977).

3.3.5. Red turpentine beetle

A total of 739 trees (8.9% of all trees) were colonized by RTB of which 76.5% survived, the remainder being classified as dead due to direct mortality attributed to fire effects or indirect mortality attributed to attacks by other bark beetle species. It is well-established that RTB colonizes fire-injured trees (Parker et al., 2006), particularly *P. ponderosa* (Fettig et al., 2008, 2010), and there is a concern that RTB populations could increase in fire-injured trees and attack adjacent apparently healthy trees (e.g., Ferrell, 1996; Ganz et al., 2003), or predispose trees to attack by other bark beetle species (Bradley and Tueller, 2001). Overall, significantly more trees were colonized by RTB on early and late season burns compared to the untreated control (all trees; $F_{2,6} = 5.3$, $P = 0.047$; Fig. 8). No significant difference was observed between early and late season burns (Fig. 8). A significant treatment effect was also observed for the 45.7 cm dbh class ($F_{2,6} = 5.8$, $P = 0.039$) in which significantly more trees were colonized by RTB on early season burns than the untreated control (Fig. 8), which differed with the 15.2 cm dbh class (Fig. 8). Fettig et al. (2008) reported >98% of pines that were attacked by RTB occurred on burned plots in the northern Sierra Nevada, but no tree mortality was attributed to these attacks. Few (10 trees) trees were attacked by RTB in the untreated control, and no attacks occurred within the two largest dbh classes in this treatment (Fig. 8). Based on Fettig et al. (2010), we feel any negative impacts by large numbers of RTB attacks following prescribed burns would have been captured during the 3-yr period.

Fettig et al. (2004a) reported that a single peak in RTB flight activity occurs in late May through early June in the Sierra Nevada. The beetle is capable of overwintering as an adult and there is often a period in early spring when large numbers of adults are captured. It is at this time that RTB is likely searching for viable hosts and therefore treatments such as prescribed burns (Fig. 8) and mechanical fuel treatments (Fettig et al., 2006) that might exacer-

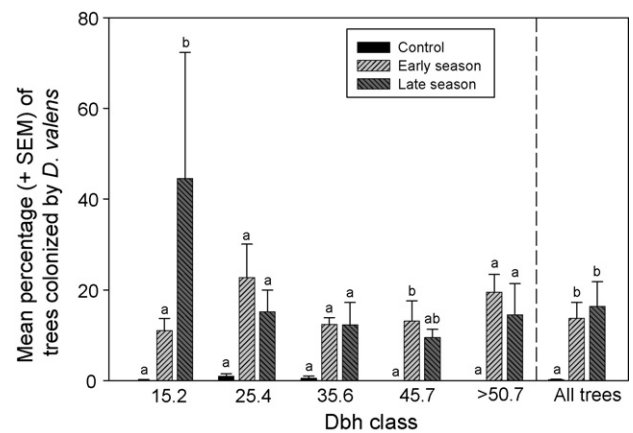


Fig. 8. Mean percentage of trees colonized by red turpentine beetle, *Dendroctonus valens* LeConte, by diameter class (mid-point of 10-cm diameter classes shown except for largest diameter class) 1 yr after prescribed burns were implemented, Tahoe National Forest, California, USA. Means (+SEM) followed by the same letter within groups are not significantly different (Tukey's HSD, $P > 0.05$). Tree mortality was not attributed to *D. valens*.

bate attraction typically result in higher levels of RTB attacked trees when implemented just prior to peak flight activity.

3.3.6. Root pathogens associated with bark beetles

We found Ophiostomatoid fungi belonging to the genera *Leptographium* and *Sporothrix* in root/root collar samples. The *Leptographium* isolates were morphologically consistent with descriptions of *L. terebrantis* S.J. Barras and T.J. Perry. *Leptographium wagneri* (W.B. Kendr.) M.J. Wingf., the cause of black stain root disease (BSRD), was not found nor was symptom consistent with BSRD infection. Black stain root disease is a serious pathogen of *P. ponderosa* and *P. jeffreyi* and is vectored by root feeding bark beetles (Schweigkofler et al., 2005). While soil and site disturbance is associated with inciting BSRD (Harrington and Cobb, 1988), little information is available on prescribed fire effects on occurrence or intensification of BSRD. In a preliminary report on BSRD in *P. ponderosa*, Otrosina et al. (2007a) reported higher levels of tree mortality in burned plots than in unburned plots, although occurrence of BSRD in burned plots declined to baseline levels 5 yr after treatment. Future studies should be conducted to more fully understand the effects of prescribed fire on this pathogen.

Of the 45 trees sampled, only eight were positive for either *Sporothrix* (two trees) or *L. terebrantis*. For either fungal genus, no seasonal burn treatment effects could be discerned in isolation frequency. Interestingly, no Ophiostomatoid fungi were isolated from control (unburned) samples or from trees having no cambium damage in burned treatments. The isolation of *Leptographium* is consistent with the incidence of RTB in this study (8.9% of all trees) and several *Leptographium* species are known associates of RTB, including *L. terebrantis* (Harrington, 1988). On the other hand, the isolation frequency in this study was surprisingly low. For example, in longleaf pine, *P. palustris* Mill., Otrosina et al. (2002) employed methods used in the present study and reported high isolation frequencies (>50%, all cases) of this group of fungi in roots following prescribed fire and fire + mechanical treatments (Otrosina et al., 1999). In the latter case, tree mortality was associated with root infection by *L. terebrantis* and *L. procerum* (W.B. Kendr.) M.J. Wingf. Relatively high frequencies (e.g., >75% for high severity wildfire) of *L. terebrantis* and *L. procerum* in lateral roots were also reported by Hanula et al. (2002) in *P. palustris* and slash pine, *P. elliotii* Englem., stands following mixed-severity wildfire. However, a follow up survey of these study plots (Hanula et al., 2002) detected no presence of *Leptographium* spp. in the roots 8 yr after the wildfire (Otrosina et

al., 2007b). In green house pathogenicity tests, *L. terebrantis* was the most pathogenic to *P. ponderosa* seedlings (Harrington and Cobb, 1983; Owen et al., 1987) in comparison to other Ophiostomatoid associates of several conifer infesting bark beetles. While RTB is generally not considered a primary tree killer its association with *L. terebrantis*, being an apparently more virulent pathogen than many other Ophiostomatoid associated with congeners such as MPB and WPB, is somewhat of an enigma. Owen et al. (1987) suggested less virulent fungal associates may be unable to effectively colonize host tissue in the lower stem region (i.e., due to resin defenses) where RTB commonly initiates attacks. It may be that infection and colonization of roots and stems by *Leptographium* after introduction by RTB is transitory. There are complex interactions between bark beetles and their fungal associates with regard to impact on disease development, tree physiology, and tree mortality that warrant further research in *P. ponderosa* and *P. jeffreyi* forests.

3.4. Temporal distributions of tree mortality

In our study, 38.1, 41.8 and 20.1% of total tree mortality (≥ 20.3 cm dbh) occurred during the first, second and third yr, respectively. Similar trends were observed for both direct and indirect tree mortality. No significant differences in levels of total mortality, direct mortality, or indirect mortality were observed among yr ($df=2,24$; $P>0.16$, all cases). On an individual plot basis, annual levels of tree mortality ranged from 0% (untreated control, plot 6; all 3 yr) to 3.7% (early season burn, plot 1; yr 1).

Breece et al. (2008) reported that prescribed burns increased bark beetle attacks on *P. ponderosa* over 3 yr from 1.5 to 13% of all trees; increased successful, lethal attacks from 0.4 to 7.6%; and increased mortality of *P. ponderosa* from all causes from 0.6 to 8.4%. Approximately 80% of all bark beetle-attacked trees were colonized during the first yr following the application of prescribed burns. Eight and 12% were colonized during the second and third yr, respectively (Breece et al., 2008). Fettig et al. (2010) reported the amount of bark beetle-caused tree mortality was evenly distributed 2 and 4 yr after the application of thinning and burning treatments in the Southern Cascades. In their study, only one of five analyses yielded a significant temporal effect on prescribed burned units (i.e., burned and thinned + burned) in which significantly higher levels of bark beetle-caused tree mortality occurred 2 yr after the application of prescribed burns in the smallest diameter class (Fettig et al., 2010). It is possible that we have not captured all tree mortality attributed to burn effects during this 3-yr period.

4. Management implications

Since 1999, ~800,000 wildland fires have burned ~28 million ha in the USA (NIFC, 2009). Generally, fewer wildfires are affecting larger areas at increased intensities and severities than during prior decades. Such events emphasize the need for well-designed silvicultural treatments to reduce their extent and severity. We demonstrated that significantly higher levels of tree mortality (all sources) occurred following early and late season burns compared to the untreated control, however no significant difference was observed between burn treatments (all trees; Fig. 2). Most of the mortality was concentrated in the smallest diameter class (<20.2 cm dbh, Table 3). For the largest trees (>50.7 cm dbh), significantly higher levels of tree mortality occurred on early season burns than the untreated control ($F_{2,6}=5.5$; $P=0.044$), most of which resulted from indirect mortality attributed to bark beetle attacks (Fig. 4), specifically WPB and MPB (Figs. 6 and 7). Ten large trees (>50.7 cm dbh) were killed by WPB following early season burns, including the largest in our study (101 cm dbh). However, this mortality represents <1 tree/ha in these plots while manage-

ment standards recommend 4.9 and 7.4 snags/ha (with a minimum dbh of 46 cm) in *P. ponderosa* and mixed-conifer forests in portions of the southwestern USA, respectively (Ganey, 1999; Stephens, 2004). In the nearby Lake Tahoe Basin old-growth forest structure is reported to have a minimum of 5 snags/ha that are >76 cm dbh (Barbour et al., 2002). Stephens (2004) reported ~4 snags/ha for *P. jeffreyi* mixed-conifer forests in the Sierra San Pedro Martir National Park, Mexico, an area that has not experienced systematic fire suppression. In our study, WPB created most large-diameter snags (11 of 15) generated during the 3-yr period. Furthermore, we found no large-diameter snags that had been recently killed (i.e., within 2 yr by presence of crown fade) during our initial census. Few (<1 /ha) older snags (>2 yr) were observed, suggesting that these stands were, and likely will be, snag deficient for some time. To that end, while some forest managers may be concerned by levels of WPB-caused tree mortality in large-diameter trees following early season burns, this mortality was not extensive and increased snag densities toward target thresholds. Snags are important nesting, roosting and foraging habitats for a variety of wildlife (Scott et al., 1977; Bull et al., 1997). Many bird species exhibit a preference for larger (>50 cm dbh) and taller (>15 m in height) snags (Laudenslayer, 2002; Lehmkuhl et al., 2003).

Precipitation patterns were normal during this study (Fig. 1) and overall bark beetle activity levels were considered low to moderate (USDA Forest Service, 2006, 2008). Furthermore, stand densities in our study were low to moderate for *P. ponderosa* and *P. jeffreyi* forests (10.4–25.5 m²/ha on an individual plot basis, Table 1; Youngblood et al., 2004). Factors such as stand density, tree diameter and host density are consistently identified as primary attributes associated with bark beetle infestations (reviewed by Fettig et al., 2007). In this context, we caution the reader that the amount of indirect mortality attributed to bark beetle attacks in this study may be a conservative estimate, particularly in comparison to the application of these treatments in more dense stands or during extended periods of drought.

A primary objective of using prescribed fire in *P. ponderosa* and *P. jeffreyi* forests is to reduce surface fuel loadings and densities of small trees (e.g., <20.2 cm dbh) that serve as ladder fuels and permit surface fires to become crown fires, while limiting undesirable levels of mortality within the larger diameter classes. A second objective is to increase the relative proportion of fire-tolerant tree species such as *P. ponderosa* and *P. jeffreyi*. However, this objective is of limited relevance in the current study as stands were almost pure *P. ponderosa* and *P. jeffreyi* (Table 1). In our study, early and late season burns were equally effective at reducing fine surface fuels (≤ 10 -h fuels) and ladder fuels (i.e., small trees that provide vertical continuity between surface and canopy fuels; Fig. 2), but late season burns were more effective at reducing large downed woody fuels (>10 -h fuels) (Table 2). Few meaningful differences in levels of indirect tree mortality attributed to bark beetle attack were observed between early and late season burns. We conclude that late season prescribed burns may be more effective at achieving overall management goals, but that early concerns regarding increased levels of indirect tree mortality following early season burns are unwarranted during the conditions under which this study was executed. Further research is necessary to determine how early and late season burns would achieve the objectives described above under different site and stand conditions (e.g., under high stand densities) where the potential for more severe tree injuries is greater.

Acknowledgements

We thank R. Borys, C. Dabney, S. Hamud, D. Huber, P. Jiroš, J. Lee, and S. Seybold (Pacific Southwest Research Station, USDA Forest Service), J. Egan, E. Frolli, A. Garcia, R. Mahnke, S. McFarland, and

L. Yazzie (Forest Health Protection, USDA Forest Service), C. Mautner (University of California), M. Patterson (University of Reno), A. Piscitelli (Humboldt State University), C. Stoll (Chico State University) and J. Young (Oregon State University) for technical assistance. In addition, we are grateful to the staff of the Truckee and Sierraville Ranger Districts, Tahoe National Forest (USDA Forest Service) for providing the study site, and specifically to B. Melville (Truckee Ranger District) for implementing the prescribed burns according to study protocols. A special thanks to C. Hayes (Pacific Southwest Research Station) and S. Hood (Rocky Mountain Research Station, USDA Forest Service) for their critiques, which greatly improved an earlier version of this manuscript. This research was supported, in part, by a Special Technology and Development Program grant (R5–2004–01) to C.J.F., S.L.S., and D.L.C., a U.S. President's Early Career Award for Scientists and Engineers to C.J.F., the Pacific Southwest Research Station and Northeastern California Forest Health Protection group.

References

- Agee, J.K., 1993. Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. *Northwest Sci.* 65, 188–199.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211, 83–96.
- Arno, S.F., 1980. Forest fire history of the northern Rockies. *J. For.* 78, 460–465.
- Barbour, M., Kelley, E., Maloney, P., Rizzo, D., Royce, E., Fites-Kaufmann, J., 2002. Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada US. *J. Veg. Sci.* 13, 461–472.
- Bradley, T., Tueller, P., 2001. Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe Basin. *For. Ecol. Manage.* 142, 205–214.
- Breece, C.R., Kolb, T.E., Dickson, B.G., McMillin, J.D., Clancy, K.M., 2008. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. *For. Ecol. Manage.* 255, 119–128.
- Brown, J.K., 1974. Handbook for Inventorying Downed Woody Material. INT-GTR-16. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, 24 pp.
- Bull, E.L., Parks, C.G., Torgensen, T.R., 1977. Trees and Logs Important to Wildlife in the Interior Columbia River Basin. PNW-GTR-391. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 55 pp.
- Burns, R.M., Honkala, B.H., 1990. Silvics of North America. Vol. I. Conifers. Agric. Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, 675 pp.
- Cahill, T.A., Carroll, J.J., Campbell, D., Gill, T.E., 1996. Air quality. In: Sierra Nevada Ecosystem Project: Final Report to Congress. Vol. II: Assessments and Scientific Basis for Management Options. Water Resources Center Report No. 37. Centers for Water and Wildland Resources, University of California, Davis, pp. 1227–1260.
- Covington, W.W., Moore, M., 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47.
- DeGomez, T., Fettig, C.J., McMillin, J.D., Anhold, J.A., Hayes, C., 2008. Managing Slash to Minimize Colonization of Residual Leave Trees by *Ips* and Other Bark Beetle Species Following Thinning in Southwestern Ponderosa Pine. Bull. AZ1448. University of Arizona, College of Agriculture and Life Sciences, Tucson, AZ, 21 pp.
- Elkin, C.M., Reid, M.L., 2004. Attack and reproductive success of mountain pine beetles (Coleoptera: Scolytidae) in fire-damaged lodgepole pines. *Environ. Entomol.* 33, 1070–1080.
- Evans, W.G., 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* DeGeer (Coleoptera: Buprestidae). *Ann. Entomol. Soc. Am.* 59, 873–877.
- Ferrell, G.T., 1996. The influence of insect pests and pathogens on Sierra forests. In: Sierra Nevada Ecosystem Project: Final Report to Congress, vol II. Assessments and Scientific Basis for Management Options. University of California, Davis, Centers for Water and Wildland Resources, pp. 1177–1192.
- Fettig, C.J., Borys, R.R., Cluck, D.R., Smith, S.L., 2004a. Field responses of *Dendroctonus valens* (Coleoptera: Scolytidae) and a major predator, *Temnochila chlorodia* (Coleoptera: Trogositidae), to host kairomones and a bark beetle pheromone. *J. Entomol. Sci.* 39, 490–499.
- Fettig, C.J., Shea, P.J., Borys, R.R., 2004b. Seasonal flight patterns of four bark beetle species (Coleoptera: Scolytidae) along a latitudinal gradient in California. *Pan-Pacific Entomol.* 80, 4–17.
- Fettig, C.J., Shea, P.J., Borys, R.R., 2005. Spatial and temporal distributions of four bark beetle species (Coleoptera: Scolytidae) along two elevational transects in the Sierra Nevada. *Pan-Pacific Entomol.* 81, 6–19.
- Fettig, C.J., McMillin, J.D., Anhold, J.A., Hamud, S.M., Borys, R.R., Dabney, C.P., Seybold, S.J., 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. *For. Ecol. Manage.* 230, 55–68.
- Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. *For. Ecol. Manage.* 238, 24–53.
- Fettig, C.J., Borys, R.R., McKelvey, S.R., Dabney, C.P., 2008. Blacks Mountain Experimental Forest: bark beetle response to differences in forest structure and the application of prescribed fire in interior ponderosa pine. *Can. J. For. Res.* 38, 924–935.
- Fettig, C.J., Borys, R.R., Dabney, C.P., 2010. Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades, California. *For. Sci.* 56, 60–73.
- Fischer, W.C., 1980. Prescribed fire and bark beetle attack in ponderosa pine forests. *Fire Manage. Notes* 41, 10–12.
- Fowler, J.F., Sieg, C.H., 2004. Postfire Mortality of Ponderosa Pine and Douglas-fir: A Review of Methods to Predict Tree Death. RMRS-GTR-132. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 25 pp.
- Fulé, P.Z., Covington, W.W., Smith, H.B., Springer, J.D., Heinlein, T.A., Huisinga, K.D., Moore, M.M., 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. *For. Ecol. Manage.* 170, 19–41.
- Furniss, R.L., Carolin, V.M., 1977. Western Forest Insects. Misc. Pub. 1339. U.S. Department of Agriculture, Forest Service, Washington, DC, 654 pp.
- Ganey, J.L., 1999. Snag density and composition of snags populations on two National Forests in northern Arizona. *For. Ecol. Manage.* 117, 169–178.
- Ganz, D.J., Dahlsten, D.L., Shea, P.J., 2003. The post-burning responses of bark beetles to prescribed burning treatments. In: Omi, P.N., Joyce, L.A. (Eds.), *Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings. RMRS-P-29*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, pp. 143–158.
- Hanula, J.L., Meeker, J.R., Miller, D.R., Barnard, E.L., 2002. Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. *For. Ecol. Manage.* 170, 233–247.
- Hare, R.C., 1961. Heat Effects on Living Plants. SO-OC-183. U.S. Department of Agriculture, Forest Service, Southern Research Station, New Orleans, LA, 32 pp.
- Harrington, M., 1993. Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. *Int. J. Wildland Fire* 3, 65–72.
- Harrington, T.C., Cobb Jr., F.W., 1983. Pathogenicity of *Leptographium* and *Verticillidiella* spp. isolated from roots of western North American conifers. *Phytopathology* 73, 596–599.
- Harrington, T.C., 1988. *Leptographium* species, their distributions, hosts, and insect vectors. In: Harrington, T.C., Cobb Jr., F.W. (Eds.), *Leptographium Root Diseases on Conifers*. APS Press, St. Paul, MN, pp. 1–40.
- Harrington, T.C., Cobb Jr., F.W., 1988. *Leptographium* Root Diseases on Conifers. American Phytopathological Society, St. Paul, MN, 149 pp.
- Hood, S.M., Smith, S.L., Cluck, D.R., 2007. Delayed conifer tree mortality following fire in California. In: Powers, R.F. (Ed.), *Restoring Fire-adapted Ecosystems: Proceedings of the 2005 National Silviculture Workshop. PSW-GTR-203*. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 261–283.
- Hood, S.M., Cluck, D.R., Smith, S.L., Ryan, K.C., 2008. Using bark char codes to predict post-fire cambium mortality. *Fire Ecol.* 4, 57–73.
- Hough, W.A., 1968. Carbohydrate reserves of saw-palmetto: seasonal variation and effects of burning. *For. Sci.* 14, 399–405.
- Kegley, S.J., Livingston, R.L., Gibson, K.E., 1997. Pine Engraver, *Ips pini* (Say), in the United States. FIDL 122. U.S. Department of Agriculture, Forest Service, Washington, DC, 5 pp.
- Kilgore, B., 1973. The ecological role of fire in sierran conifer forests: its application to National Park management. *Q. Res.* 3, 496–513.
- Kilgore, B.M., Taylor, D., 1979. Fire history of a sequoia mixed conifer forest. *Ecology* 60, 129–142.
- Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological Effects of Prescribed Fire Season: a Literature Review and Synthesis for Managers. PSW-GTR-224. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Berkeley, CA, 80 pp.
- Kolb, T.E., Guerard, N., Hofstetter, R.W., Wagner, M.R., 2006. Attack preference of *Ips pini* on *Pinus ponderosa* in northern Arizona: tree size and bole position. *Agric. For. Entomol.* 8, 295–303.
- Kolb, T.E., Agee, J.K., Fulé, P.Z., McDowell, N.G., Pearson, K., Sala, A., Waring, R.H., 2007. Perpetuating old growth ponderosa pine. *For. Ecol. Manage.* 249, 141–157.
- Laudenslayer Jr., W.F., 2002. Cavity-nesting bird use of snags in eastside pine forests of northeastern California. In: Laudenslayer, W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Eds.), *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests. PSW-GTR-181*. U.S. Department of Agriculture, Forest Service, Berkeley, CA, pp. 223–236.
- Lehmkuhl, J.F., Everett, R.L., Schellhass, R., Ohlson, P., Keenum, D., Reisterer, H., Spurbeck, D., 2003. Cavities in snags along a wildfire chronosequence in eastern Washington. *J. Wildlife Manage.* 67, 219–228.
- Li, J.S., Chang, G.B., Song, Y.S., Wang, Y.W., Chang, B.S., 2001. Control project of red turpentine beetle (*Dendroctonus valens*). *For. Pest. Dis.* 4, 41–44.
- Maloney, P.E., Smith, T.F., Jensen, C.E., Innes, J., Rizzo, D.M., North, M.P., 2008. Initial tree mortality and insect and pathogen response to fire and thinning restoration treatments in an old-growth mixed-conifer forest of the Sierra Nevada, California. *Can. J. For. Res.* 38, 3011–3020.
- Martin, R.E., 1963. A basic approach to fire injury of tree stems. *Proc. Tall Timbers Fire Ecol. Conf.* 3, 151–161.
- McHugh, C.W., Kolb, T.E., 2003. Ponderosa pine mortality following fire in northern Arizona. *Int. J. Wildland Fire* 12, 7–22.

- McHugh, C.W., Kolb, T.E., Wilson, J.L., 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environ. Entomol.* 32, 510–522.
- Miller, J.M., Patterson, J.E., 1927. Preliminary studies on the relation of fire injury to bark-beetle attack in western yellow pine. *J. Agric. Res.* 34, 597–613.
- Miller, J.M., Keen, F.P., 1960. Biology and Control of the Western Pine Beetle. Misc. Pub. 800. U.S. Department of Agriculture, Forest Service, Washington, DC, 381 pp.
- National Interagency Fire Center (NIFC), 2009. Available from <http://www.nfic.gov/fire.info/> [accessed 29 January 2010].
- Negrón, J.F., McMillin, J.D., Anhold, J.A., Coulson, A., 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona USA. *For. Ecol. Manage.* 257, 1353–1362.
- Oliver, W.W., 2000. Ecological Research at the Blacks Mountain Experimental Forest in Northeastern California. PSW-GTR-179. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Berkeley, CA, 66 pp.
- Otrosina, W.J., Bannwart, D.L., Roncadori, R.W., 1999. Root infecting fungi associated with a decline of longleaf pine in the southeastern United States. *Plant Soil* 217, 145–150.
- Otrosina, W.J., Walkinshaw, C.H., Zarnoch, S.J., Sung, S.-J.S., Sullivan, B.T., 2002. Root disease, longleaf pine mortality and prescribed burning. In: Outcalt, K.W. (Ed.), *Proceedings of Eleventh Biennial Southern Silvicultural Research Conference. SRS-GTR-48*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 551–557.
- Otrosina, W.J., Spaine, P., Cook, C.D., 2007a. Incidence of Ophiostomatoid species in roots of longleaf and slash pine 1 and 8 years after a large-scale wildfire. *Phytopathology* 97, S88.
- Otrosina, W.J., Kliejunas, J.T., Smith, S., Cluck, D.R., Sung, S.S., Cook, C.D., 2007b. Blackstain root disease studies on ponderosa pine: parameters and disturbance treatments affecting infection and mortality. *Acta Silv. Lign. Hung., Spec. Ed.* 2007, 247–251.
- Owen, D.R., Lindahl, K.Q., Wood, D.L., Parmeter, J.R., 1987. Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicornis*, and *D. ponderosae* to ponderosa pine seedlings. *Phytopathology* 77, 631–636.
- Parker, T.J., Clancy, K.M., Mathiasen, R.L., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agric. For. Entomol.* 8, 167–189.
- Person, H.L., 1928. Tree selection by the western pine beetle. *J. For.* 26, 564–578.
- Peterson, D.L., Ryan, K.C., 1986. Modeling post-fire conifer mortality for long-range planning. *Environ. Manage.* 10, 797–808.
- Pollet, J., Omi, P.N., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *Int. J. Wildland Fire* 11, 1–10.
- Pyne, S.J., Andrews, P.L., Laven, R.D., 1996. *Introduction to Wildland Fire*. John Wiley & Sons Inc., NY, 808 pp.
- Rappaport, N.G., Owen, D.R., Stein, J.D., 2001. Interruption of semiochemical-mediated attraction of *Dendroctonus valens* (Coleoptera: Scolytidae) and selected nontarget insects by verbenone. *Environ. Entomol.* 30, 837–841.
- Rasmussen, L.A., Amman, G.D., Vandygriff, J.C., Oakes, R.D., Munson, A.S., Gibson, K.E., 1996. Bark Beetle and Wood Borer Infestations in the Greater Yellowstone Area During Four Postfire Years. INT-RP-487. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, 10 pp.
- Regelbrugge, J.C., Conard, S.G., 1993. Modeling tree mortality following wildfire in *Pinus ponderosa* forests in the central Sierra Nevada of California. *Int. J. Wildland Fire* 3, 139–148.
- Ryan, K.C., Reinhardt, E.D., 1988. Predicting post-fire mortality of seven western conifers. *Can. J. For. Res.* 18, 1291–1297.
- Ryan, K.C., Peterson, D.L., Reinhardt, E.D., 1988. Modeling long-term fire caused mortality of Douglas-fir. *For. Sci.* 34, 190–199.
- Sánchez-Martínez, G., Wagner, M.R., 2002. Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. *For. Ecol. Manage.* 170, 145–160.
- Schweigkofler, W., Otrosina, W.J., Smith, S.L., Cluck, D.R., Maeda, K., 2005. Detection and quantification of *Leptographium wagneri*, the cause of black-stain root disease, from bark beetles (Coleoptera: Scolytidae) in northern California using regular and real-time PCR. *Can. J. For. Res.* 35, 1798–1808.
- Schwilk, D.W., Knapp, E.E., Ferrenberg, S.M., Keeley, J.E., Caprio, A.C., 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. *For. Ecol. Manage.* 232, 36–45.
- Scott, V.E., Evans, K.E., Patton, D.R., Stone, C.P., 1977. *Cavity-Nesting Birds of North American Forests*. Agric. Handbook 511. U.S. Department of Agriculture, Forest Service, Washington, DC, 122 pp.
- Seybold, S.J., Huber, D.P.W., Lee, J.C., Graves, A.D., Bohlmann, J., 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochem. Rev.* 5, 143–178.
- Sieg, C.H., McMillin, J.D., Fowler, J.F., Allen, K.K., Negrón, J.F., Wadleigh, L.L., Anhold, J.A., Gibson, K.E., 2006. Best predictors for postfire mortality of ponderosa pine trees in the Intermountain West. *For. Sci.* 52, 718–728.
- Skinner, C.N., Chang, C., 1996. Fire regimes, past and present. In: *Sierra Nevada Ecosystem Project: Final Report to Congress. Vol. II: Assessments and Scientific Basis for Management Options*. Water Resources Center Report No. 37. Centers for Water and Wildland Resources, University of California, Davis, pp. 1041–1069.
- Smith, S.L., Borys, R.R., Shea, P.J., 2009. Jeffrey Pine Beetle. FIDL 11. U.S. Department of Agriculture, Forest Service, Portland, OR, 8 pp.
- Stephens, S.L., 2004. Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine – mixed conifer forest in northwestern Mexico. *For. Ecol. Manage.* 199, 103–113.
- Stephens, S.L., Ruth, L.W., 2005. Federal forest-fire policy in the United States. *Ecol. Apps.* 15, 532–542.
- Stephens, S.L., Skinner, C.N., Gill, S.J., 2003. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. *Can. J. For. Res.* 33, 1090–1101.
- Swetnam, T.W., 1990. Fire history and climate in the southwestern United States. In: Krammes, J.S. (Ed.), *Effects of Fire Management on Southwestern Natural Resources. Proceedings of the Symposium. November 15–17, 1988, Tucson, AZ. RM-GTR-191*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, pp. 6–17.
- Swetnam, T.W., Baisan, C.H., 2002. Tree-ring reconstructions of fire and climate history in the Sierra Nevada and southwestern United States. In: Veblen, T.T., Baker, W., Montenegro, G., Swetnam, T.W. (Eds.), *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. Springer-Verlag, NY, p. 465.
- Swezy, D.M., Agee, J.K., 1991. Prescribed fire effects on fine-root and tree mortality in old-growth ponderosa pine. *Can. J. For. Res.* 21, 626–634.
- Taylor, A.H., 2000. Fire regimes and forest changes along a montane forest gradient, Lassen Volcanic National Park, southern Cascade Mountains, USA. *J. Biogeography* 27, 87–104.
- Taylor, A.H., Skinner, C.N., 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California USA. *For. Ecol. Manage.* 111, 285–301.
- Thies, W.G., Westlund, D.J., Loewen, M., 2005. Season of prescribed burn in ponderosa pine forests in eastern Oregon: impact on pine mortality. *Int. J. Wildland Fire* 14, 223–231.
- USDA Forest Service, 2006. Forest pest conditions in California – 2005. Available from <http://www.fs.fed.us/r5/spf/publications/pestconditions/> [accessed 18 March 2009].
- USDA Forest Service, 2008. Forest pest conditions in California – 2007. Available from <http://www.fs.fed.us/r5/spf/publications/pestconditions/> [accessed 18 March 2009].
- van Wagtenonk, J.W., 1972. *Fire and Fuel Management Relationships in Mixed Conifer Ecosystems of Yosemite National Park*. Ph.D. Dissertation, University of California, Berkeley, CA, 163 pp.
- van Wagtenonk, J.W., Benedict, J.M., Sydoriak, W.M., 1996. Physical properties of woody fuel particles of Sierra Nevada conifers. *Int. J. Wildland Fire* 6, 103–186.
- Wallin, K.F., Kolb, T.E., Skov, K.R., Wagner, M.R., 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environ. Entomol.* 32, 652–661.
- Wickman, B.E., 1964. Attack habits of *Melanophila consupta* on fire-killed pines. *Pan Pacific Entomol.* 40, 183–186.
- Youngblood, A., Max, T., Coe, K., 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. *For. Ecol. Manage.* 199, 191–217.