Blacks Mountain Experimental Forest: bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine[1]

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Abstract: Mechanical thinning and the application of prescribed fire are commonly used tools in the restoration of fire-adapted forest ecosystems. However, few studies have explored their effects on subsequent amounts of bark beetle caused tree mortality in interior ponderosa pine, *Pinus ponderosa* Dougl. ex P. & C. Laws. var. *ponderosa*. In this study, we examined bark beetle responses to creation of midseral (low diversity) and late-seral stages (high diversity) and the application of prescribed fire on 12 experimental units ranging in size from 76 to 136 ha. A total of 9500 (5.0% of all trees) *Pinus* and *Abies* trees died 2 years after treatment of which 28.8% (2733 trees) was attributed to bark beetle colonization. No significant difference in the mean percentage of trees colonized by bark beetles was found between low diversity and high diversity. The application of prescribed fire resulted in significant increases in bark beetle caused tree mortality (all species) and for western pine beetle, *Dendroctonus brevicomis* LeConte, mountain pine beetle, *Dendroctonus ponderosae* Hopkins, *Ips* spp., and fir engraver, *Scolytus ventralis* LeConte, individually. Approximately 85.6% (2339 trees) of all bark beetle caused tree mortality occurred on burned split plots. The implications of these and other results to sustainable forest management are discussed.

Résumé : L'éclaircie mécanisée et le brûlage dirigé sont des outils couramment utilisés pour restaurer les écosystèmes adaptés au feu. Cependant, peu d'études ont examiné leurs effets sur l'ampleur subséquente de la mortalité causée par les scolytes chez le pin ponderosa typique, *Pinus ponderosa* Dougl. ex P. & C. Laws. var. *ponderosa*. Dans cette étude, nous examinons la réaction des scolytes à la création de forêts aux stades de milieu de succession écologique (faible diversité) et aux derniers stades de succession écologique (forte diversité) ainsi qu'à l'utilisation du brûlage dirigé dans 12 unités expérimentales dont la dimension varie de 76 à 136 ha. Un total de 9 500 tiges de *Pinus* et d'*Abies* (5,0 % de tous les arbres) étaient mortes 2 ans après les traitements. De ce nombre, la mort de 28,8 % des tiges (2 733 arbres) a été attribuée à la colonisation par les scolytes. Aucune différence significative dans le pourcentage d'arbres colonisés par les scolytes n'a été observée entre les traitements faible diversité et forte diversité. L'utilisation du brûlage dirigé a entraîné une augmentation significative de la mortalité causée par toutes les espèces de scolytes et en particulier par le dendroctone occidental du pin, *Dendroctonus brevicomis* LeConte, le dendroctone du pin ponderosa, *Dendroctonus ponderosae* Hopkins, *Ips* spp. et le scolyte du sapin, *Scolytus ventralis* LeConte. Approximativement 85,6 % (2 339 arbres) de toute la mortalité causée par les scolytes est survenue dans la portion brûlée des parcelles expérimentales. La discussion porte sur les implications de ces résultats et d'autres sur l'aménagement forestier durable.

[Traduit par la Rédaction]

Introduction

Bark beetles (Coleoptera: Curculionidae, Scolytinae), a large and diverse group of insects consisting of approximately 550 species in North America, are commonly recognized as important mortality agents in western coniferous forests (Furniss and Carolin 1977). Most species feed on the phloem tissue of woody plants, often directly killing the host, thus influencing forest ecosystem structure and function by regulating certain aspects of primary production, nutrient cycling, ecological succession, and the size, distribution, and abundance of forest trees (Mattson 1977). Bark beetle infestations may impact timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, real estate values, biodiversity, endangered species, and cultural resources.

Resource managers are challenged to maintain forests for a variety of uses. Sound management strategies require

Received 15 May 2007. Accepted 10 December 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 21 April 2008.

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[1]This article is one of a selection of papers from the Special Forum on Ecological Studies in Interior Ponderosa Pine — First Findings from Blacks Mountain Interdisciplinary Research.

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 doi:10.1139/X07-243

knowledge about the resiliency of these ecosystems to both allogenic and autogenic disturbances. This is particularly true of the interior ponderosa pine, *Pinus ponderosa* Dougl. ex P. & C. Laws. var. *ponderosa*, type in California (SAF 237) where, among other factors, past effects of highly effective fire suppression and differential cuttings of large-diameter, fire-tolerant tree species, such as ponderosa and Jeffrey pine, *Pinus jeffreyi* Grev. & Balf., have resulted in substantial changes in forest structure and composition (Oliver 2000). Prior to Euro-American settlement, open park-like forests of widely dispersed ponderosa and Jeffrey pines were common, particularly on xeric sites. Frequent thinning of small-diameter 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). Compared with presettlement conditions, today's forests are denser, have more smaller trees and fewer larger trees, and are dominated by more shade-tolerant and fire-intolerant species such as white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. High stand densities increase competition among trees for growing space (Reineke 1933), thereby increasing their susceptibility to bark beetles and other forest insects and diseases. At times, bark beetle populations have caused significant amounts of tree mortality in interior ponderosa pine, particularly during periods of drought (Furniss and Carolin 1977). Extensive amounts of bark beetle caused tree mortality may exacerbate problems associated with heavy fuel loads (Covington and Moore 1994). In recent years, unusually large and severe wildfires in the western United States have aroused public concern and have manifested the need for well-designed silvicultural treatments to reduce their extent and severity.

Interior ponderosa pine forests are recognized for the diversity of tree-killing bark beetle species inhabiting them (Oliver 2000), most notably western pine beetle (WPB), *Dendroctonus brevicomis* LeConte, mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, Jeffrey pine beetle (JPB), *Dendroctonus jeffreyi* Hopkins, pine engraver (PE), *Ips pini* (Say), and fir engraver (FE), *Scolytus ventralis* LeConte. Western pine beetle is a major cause of ponderosa pine mortality throughout much of the western United States and particularly in California. Under certain conditions, such as extended drought, WPB can attack and kill apparently healthy trees of all ages and size classes (Miller and Keen 1960). Mountain pine beetle is the most destructive bark beetle in western North America (Furniss and Carolin 1977), ranging throughout British Columbia, Alberta, most of the western United States, and into northern Mexico where it colonizes several pines in addition to ponderosa pine, most notably lodgepole pine, *Pinus contorta* Dougl. ex Loud., sugar pine, *Pinus lambertiana* Dougl., and western white pine, *Pinus monticola* Dougl. ex D. Don (Furniss and Carolin 1977). Jeffrey pine beetle is the major bark beetle pest of Jeffrey pine and usually attacks individual mature trees. During epidemics, group kills of 20–30 trees are common (Furniss and Carolin 1977). Pine engraver has a transcontinental distribution and is one of the most common bark beetle species in North America (Kegley et al. 1997). Outbreaks are often short-lived but increase in duration and extent when suitable host material is plentiful and populations grow sufficiently to colonize apparently healthy trees (Kegley et al. 1997). *Ips* spp. typically colonize slash, saplings, and weakened trees or trees previously colonized by more aggressive bark beetle species. Fir engraver is the major pest of true firs, particularly white fir, in the western United States. Trees of all sizes may be attacked and killed, but outbreaks are typically associated with trees stressed by drought, defoliation, or other factors (Furniss and Carolin 1977).

Prescribed fire is used to reduce the accumulation of hazardous fuels, enhance wildlife habitat, and restore fire-adapted forest ecosystems to presettlement conditions (Agee and Skinner 2005; Fettig et al. 2007). Forest managers must plan and execute prescribed burns in a careful manner to minimize injury to desirable residual trees while still fulfilling management objectives. Sublethal heating of critical plant tissue can stress trees, which then are more susceptible to bark beetle attack (Parker et al. 2006). Wallin et al. (2003) examined relationships among fire injury, tree physiological condition, and susceptibility of ponderosa pine to bark beetles (several species) in northern Arizona. The proportion of successful colonization attempts by *Dendroctonus* and *Ips* spp. was low but generally positively related to intensity of crown scorch. Similarly, others have reported that crown scorch and consumption volume are important variables in discriminating between ponderosa pines that survived and those that died following mixed-severity wildfires (Sieg et al. 2006; Hood et al. 2007). In the central Sierra Nevada, Schwilk et al. (2006) found that the probability of bark beetle attack (several species) on pines did not differ between early- and late-season burns, while probability of attack on firs was greater following early-season burns. Bark beetle attacks occurred more frequently on burned plots than on untreated controls. The propensity for bark beetles to attack fire-damaged trees has led to questions regarding how the amount and distribution of bark beetle caused tree mortality will be affected by large-scale restoration of fire-adapted forest ecosystems with prescribed fire (Ganz et al. 2003; Fettig 2004). Furthermore, concerns have been expressed about the potential for bark beetle populations to increase in fire-affected trees and then colonize apparently healthy trees in adjacent areas but have not been realized in some studies (Hanula et al. 2002). Parker et al. (2006) provided an extensive review of interactions between insects and fire (prescribed and wildfire) in coniferous forests of interior western North America, which likely has broader applicability.

Factors involving tree density are consistently associated with the occurrence and severity of bark beetle infestations in western coniferous forests (Fettig et al. 2007). One of the first published accounts was based on the supposition that ponderosa pines were less likely to succumb to MPB attack if their vigor was increased by removing competition (Eaton 1941). Later, Sartwell and Stevens (1975) established a threshold value of 34.4 m^2/ha of basal area above which stands were more susceptible to MPB infestation. Oliver (1995) reported that maximum stand density index (SDI) for even-aged ponderosa pine stands in northern California was regulated by MPB and WPB infestations. An SDI value of 230 defined a threshold for a zone of imminent bark beetle caused tree mortality within which endemic populations

Table 1. Parameters of prescribed burn treatments applied to 12 experimental units at Blacks Mountain Experimental Forest, California.

Variable	Block 1	Block 2	Block 3
Burn parameters			
Date	25 September – 5 October 1997	1–4 November 1999	18–19 October 2000
Fire direction	Head, backing, and spot fires	Head, backing, and spot fires	Head, backing, and spot fires
Climatic conditions*			
Temperature (°C)	6.7–24.4	6.1–20.0	7.2–18.3
Dew point (°C)	–10.0–7.2	–9.4–3.3	–5.0–3.9
Relative humidity (%)	15–61	18–73	25–59
Wind speed (kmh)	1.6–18	0–18	0–13
Fuel moisture (mean % ± SEM)			
Duff (<20 mm)	14.3±2.1	39.2±2.8	39.2±2.2
6–25 mm	10.5±1.3	18.2±1.1	18.1±1.1
25–75 mm	16.7±1.6	22.6±2.5	23.9±1.5
>75 mm	18.8±2.4	26.2±2.7	23.9±2.6

*Values based on conditions recorded on an hourly basis during burns.

kill a few trees but net growth is positive. Maximum SDI was defined at 365. The author stated that SDI has a distinct advantage over basal area as a measure of stand density because it is not significantly affected by age and site quality. Indeed, the threshold values reported above varied little with site productivity in Oliver's (1995) studies.

Management to reduce the susceptibility of stands to bark beetle attack must address factors related to tree density (Fettig et al. 2007). Thinning is commonly used to redistribute growing space to desirable trees, utilize anticipated mortality resulting from succession (e.g., stem exclusion), create early cash flows, setback succession, and reduce risks associated with wildfire, insects, and diseases. However, carelessly conducted harvests may result in physical damage to residual trees, soil compaction, and increased rates of windthrow. Residual leave trees may be at higher risk to infestation by subcortical insects and root pathogens following thinning. For instance, black stain root disease, *Leptographium wageneri* (Kendrick) Wingfield, is vectored by root-feeding *Hylastes* spp. beetles (Goheen and Cobb 1980; Harrington et al. 1985; Witcosky et al. 1986; Schweigkofler et al. 2005) and weevils (Witcosky et al. 1986; Schweigkofler et al. 2005). Populations of these insect vectors generally increase immediately following thinning. Several bark beetle species are attracted to slash created during thinning operations (Furniss and Carolin 1977), but useful guidelines are available to address these concerns (Fellin 1980; Parker 1991; Kegley et al. 1997).

Thinning not only affects residual tree vigor (Vité and Wood 1961; Smith 1975; Feeney et al. 1998; Wallin et al. 2004) but also the structural complexity of forest stands, which is known to influence, among other factors, microclimatic conditions (Fettig et al. 2007). For example, increased temperatures and windspeeds are common within newly thinned stands (Amman 1989; Bartos and Amman 1989; Schmid et al. 1992, 1995) and may accelerate development of certain bark beetle species and force them to overwinter in stages that are more susceptible to freezing (Amman 1973, 1989) or cause turbulences that disrupt pheromone plumes used for recruiting conspecifics during initial phases of host tree colonization (Thistle et al. 2004, 2005). Furthermore, the abundance and distribution of highly susceptible hosts following thinning are important, while it is also necessary to recognize that inciting factors, such as soil moisture deficiency, typically trigger outbreaks. Fettig et al. (2007) provided a review of tree and stand factors associated with bark beetle infestations and discussed mechanistic explanations on the effectiveness of reducing stand density for preventing bark beetle infestations.

The objective of this study is to determine the response of bark beetles to differences in forest structural complexity and the application of prescribed fire in interior ponderosa pine forests of California.

Materials and methods

Study site and treatment

In the mid-1990s, an interdisciplinary team of scientists was formed to conduct long-term ecological research (Blacks Mountain Ecological Research Project) relevant to interior ponderosa pine and managed by the Pacific Southwest Research Station, USDA Forest Service (Oliver and Powers 1998; Oliver 2000). Blacks Mountain Experimental Forest (BMEF) (40°40′N, 121°10′W; 1821 m elevation; 4168 ha), located on the Lassen National Forest, northeastern California, was chosen as the study area (Oliver 2000). The climate at BMEF is characterized by hot, dry summers and cold, moist winters with a mean temperature of 9.8 °C. The growing season is about 120 days. Annual precipitation averages 50.8 cm with most coming as snow.

Twelve experimental units, ranging in size from 76 to 136 ha, were established to examine the ecological effects of recreating two distinct forest structural types: midseral stage (low structural diversity (LoD)) and late-seral stage (high structural diversity (HiD)). Treatments were randomly assigned to four experimental units within each of three blocks. Blocking allowed for allocating variation to differences in tree composition associated with elevation gradients and year of treatment. LoD was created by removing larger overstory trees in addition to small understory trees leaving only trees of intermediate size, while HiD was attained by thinning smaller and retaining larger trees. Following harvesting, half of each unit was treated with prescribed fire (Tables 1 and 2). Although the design does not include untreated controls, several research natural areas (RNAs) ("pseudo controls") are well distributed within BMEF and permit qualitative comparisons with other treatments. BMEF

Table 2. Treatment and evaluation dates, Blacks Mountain Experimental Forest, California.

Plot No.	Plot size (ha)	Treatment*	Treatment date	Prescribed burn date	Census date†	
					Unburned	Burned
38	136	HiD	October 1996	October 1997	September 1998	August 1999
39	120	LoD	October 1996	October 1997	September 1998	September 1999
40	117	LoD	November 1998	October 2000	August 2002	July 2002
41	108	HiD	October 1996	October 1997	August 1998	August 1999
42	121	HiD	November 1997	November 1999	September 2001	August 2001
43	109	LoD	October 1996	October 1997	August 1998	August 1999
44	78	LoD	October 1997	November 1999	July 2001	August 2001
45	122	LoD	October 1997	November 1999	October 2001	October 2001
46	87	LoD	October 1998	October 2000	June 2002	June 2002
47	76	HiD	November 1997	November 1999	July 2002	July 2002
48	108	HiD	November 1998	October 2000	July 2002	July 2002
49	110	HiD	November 1998	October 2000	August 2002	August 2002

*HiD, high structural diversity or late-seral stage; LoD, low structural diversity or midseral stage (Oliver 2000).

†Units were cruised the second field season following implementation of prescribed burn treatments. Generally, this amount of time is sufficient to allow distinction between crown scorch resulting from fire and crown fade associated with tree mortality attributable to bark beetle attack.

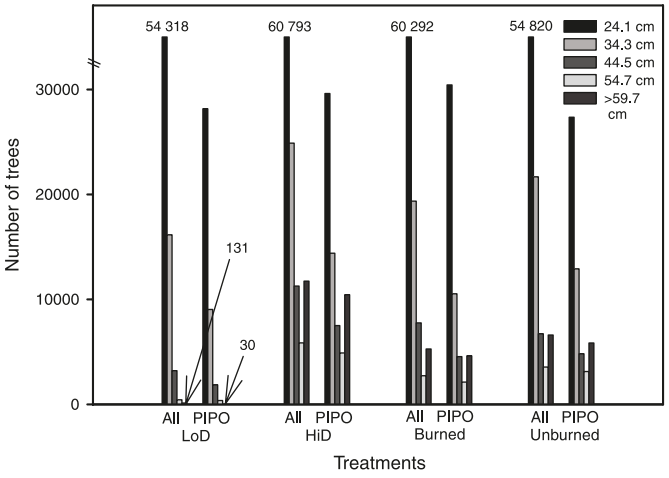
is included in grazing allotments, and therefore, six of 12 experimental units were fenced in an attempt to exclude grazing and permit analyses of the effect of grazing on several variables of interest to the interdisciplinary team. However, we viewed grazing as having no influence on bark beetle activity, particularly in the near-term, and ignored this variable in our analyses. The experimental design and a comprehensive account of treatment implementation are described in Oliver (2000).

Data collection and analyses

A 100% cruise (census) was conducted on each experimental unit to locate dead and dying pine and fir trees by presence of crown fade, an irreversible symptom of pending tree mortality. While both incense cedar, *Calocedrus decurrens* (Torr.) Florin, and western juniper, *Juniperus occidentalis* Hook., are minor components of BMEF (i.e., representing <7.7% and <0.1% of trees, respectively), these species generally are not attacked and killed by bark beetles and were ignored in surveys and subsequent analyses. In interior ponderosa pine forests, bark beetle infestations tend to be aggregated in certain microsites. Therefore, it was important to conduct a census of experimental units rather than to subsample them, which could result in inaccurate estimates of bark beetle caused tree mortality. Because of the large spatial scale of this study (1292 ha), treatment implementation (1996–2000) and thus our cruises (1998–2002) were staggered across multiple years (Table 2). In general, cruises were conducted during the second field season after the application of prescribed fire (Table 2). This amount of time is sufficient to allow distinction between crown scorch resulting from fire and crown fade associated with tree mortality attributable to bark beetle attack. All recently killed pine and fir trees >19 cm diameter at breast height (DBH) (diameter at 1.37 m height) were identified, tallied, and causal agent of mortality determined. Crown color (i.e., lime, yellow, or red) was used as an estimate of time since tree death. In interior ponderosa pine forests of California, trees with actively fading crowns (i.e., lime or yellow in color) generally died within the last 9 months. For example, ponderosa pine baited with aggregation pheromones to initiate WPB attack in July had crowns red in color 11 months later (C.J. Fettig, unpublished data). Miller and Keen (1960) provided a more detailed description of crown color in relation to WPB brood development. Tree species, DBH, crown color, colonizing bark beetle species, presence of wood borers (Coleoptera: Cerambycidae, Buprestidae), ranking of burn severity (1–4; Fettig et al. 2002), number of red turpentine beetle (RTB), *Dendroctonus valens* LeConte, attacks (pitch tubes with oxidized phloem material (i.e., reddish colored) present or granular boring dust) occurring below 1.5 m in height, and utilization by woodpeckers (bark scaling or drilling primarily from *Picoides* spp. but also *Dryocopus pileatus* (L.) and *Colaptes auratus* (L.)) were recorded. A section of bark approximately 625 cm^2 was removed with a hatchet at 2 m 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 are commonly used to distinguish among bark beetle species (Furniss and Carolin 1977). In some cases, deceased adults were available to supplement identifications based on gallery formation.

For purpose of this paper, primary variables of interest were the mean percentage of trees killed by (*i*) all causes, (*ii*) all bark beetle species across all tree species, (*iii*) individual bark beetle and tree species, (*iv*) individual bark beetle by tree species and diameter class (19–29.2, 29.3–39.3, 39.4–49.5, 49.6–59.7, and >59.7 cm DBH), (*v*) the mean percentage of trees attacked by RTB, and (*vi*) the mean number of RTB attacks per tree. The experimental design was a randomized complete block with split plots (Oliver 2000). A test of normality was performed and appropriate transformations were used when data deviated significantly from a normal distribution (Sokal and Rohlf 1995). We performed an analysis of variance on each response variable at $\alpha = 0.05$ (JMP version 3.2.6 (SAS Institute Inc., Cary, North Carolina); SigmaStat version 2.0 (SPSS Inc., Chicago, Illinois)). We limited analyses to data available from six or more (of 12) experimental units to maintain conclusions of ecological significance. 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.

Fig. 1. Number of trees (All, *Abies* and *Pinus*; PIPO, *Pinus ponderosa*) per diameter class (midpoint of 10 cm diameter classes shown except for the largest diameter class) surveyed for examining bark beetle responses to differences in forest structure and applications of prescribed fire, Blacks Mountain Experimental Forest, California. LoD, low diversity; HiD, high diversity.



Results and discussion

During this study, we surveyed a total of 188 793 pine and fir trees for mortality and bark beetle activity. Of these, 106 314 (56.3%) were ponderosa pine, 63 636 (33.7%) were white fir, and 18 843 (10.0%) were Jeffrey pine. The number of trees within individual diameter classes varied widely as a result of treatment (Fig. 1). For example, 565 and 17 593 trees occurred in the largest two diameter classes (i.e., 49.6–59.7 and >59.7 cm) in LoD and HiD, respectively. For a comprehensive account of treatment effects on stand structure and composition, see Zhang et al. (2008).

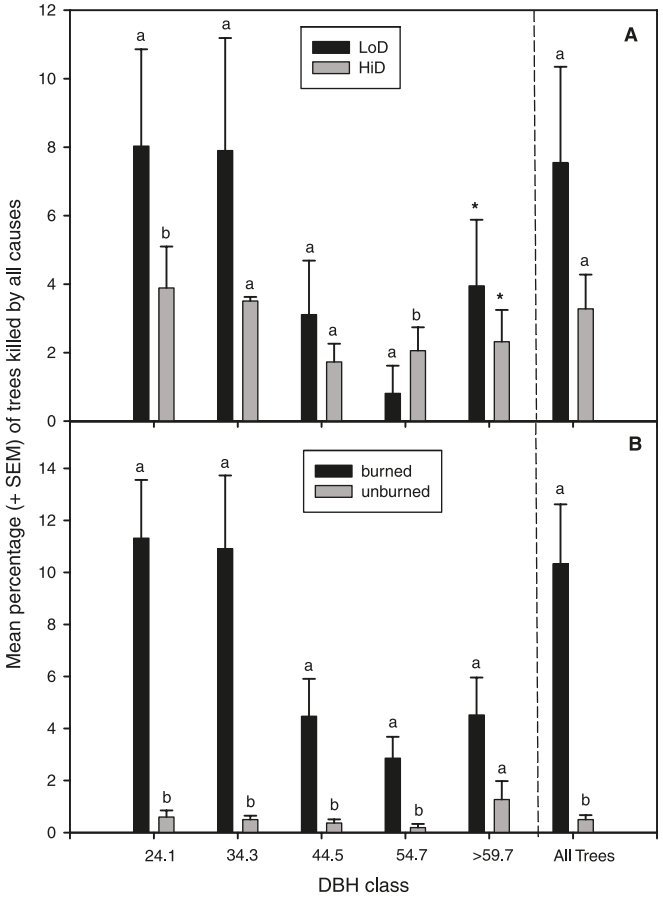
Overall tree mortality

Among all plots, a total of 9500 (5.0% of all trees) pine and fir trees died following treatment, of which 62.2% (5905 trees) occurred on LoD treatments. This figure represents mortality attributable to all sources (i.e., fire, bark beetle, mechanical, pathogen, and unidentified sources and their many interactions). Overall, no significant difference in total tree mortality was found between treatments (Fig. 2A). However, significantly more tree mortality occurred in LoD as compared with HiD in the 24.1 cm diameter class, but significantly less tree mortality occurred in LoD as compared with HiD in the 54.7 cm diameter class ($P \leq 0.04$, both cases) (Fig. 2A). No other significant differences were found (Fig. 2A). The application of prescribed fire resulted in a significant increase in total tree mortality ($F_{[1,16]} = 97.1$, $P < 0.0001$) (Fig. 2B) and within individual diameter classes ($P < 0.01$) except the largest (Fig. 2B), suggesting that trees >59.7 cm in diameter are more tolerant to such disturbances. Approximately 95% (9008 trees) of all tree mortality occurred on burned split plots.

Bark beetle responses

During this study, WPB and MPB were found colonizing ponderosa pine, JPB was found colonizing Jeffrey pine, and FE was found colonizing white fir. We also found PE and,

Fig. 2. Mean percentage of trees killed by all sources by diameter class (midpoint of 10 cm diameter classes shown except for the largest diameter class) and for all trees by (A) forest structure (LoD, low diversity; HiD, high diversity) and (B) application of prescribed fire (with and without), Blacks Mountain Experimental Forest, California. Means (+SEM) with the same letter within groups are not significantly different ($P > 0.05$). Asterisks denote that analyses were not conducted.



to a much lesser extent, emarginate ips, *Ips emarginatus* (LeConte), and *Ips latidens* (LeConte), colonizing ponderosa and Jeffrey pines. The California fivespined ips *Ips paraconfusus* Lanier, a common species along the western slope of the Sierra Nevada (Fettig et al. 2005), was not found infesting pines at BMEF and likely is not indigenous to this area (Furniss and Carolin 1977).

The precise role of each bark beetle species in causing tree mortality on our experimental units is uncertain. Nonetheless, bark beetles are considered important mortality agents following mixed-severity fires because they commonly attack trees that were weakened but not killed by fire (Parker et al. 2006). Specifically, fire-damaged ponderosa pines are susceptible to colonization by several species of bark beetle (reviewed in Parker et al. 2006). In some cases (e.g., WPB), trees must have enough green phloem and live buds to permit new needle growth for colonization and brood production to occur (Fischer 1980; Parker et al. 2006), but in others (e.g., *Hylastes* spp.), attacks are typically associated with dead trees (Furniss and Carolin 1977). In our study, attacks by several bark beetle species were ac-

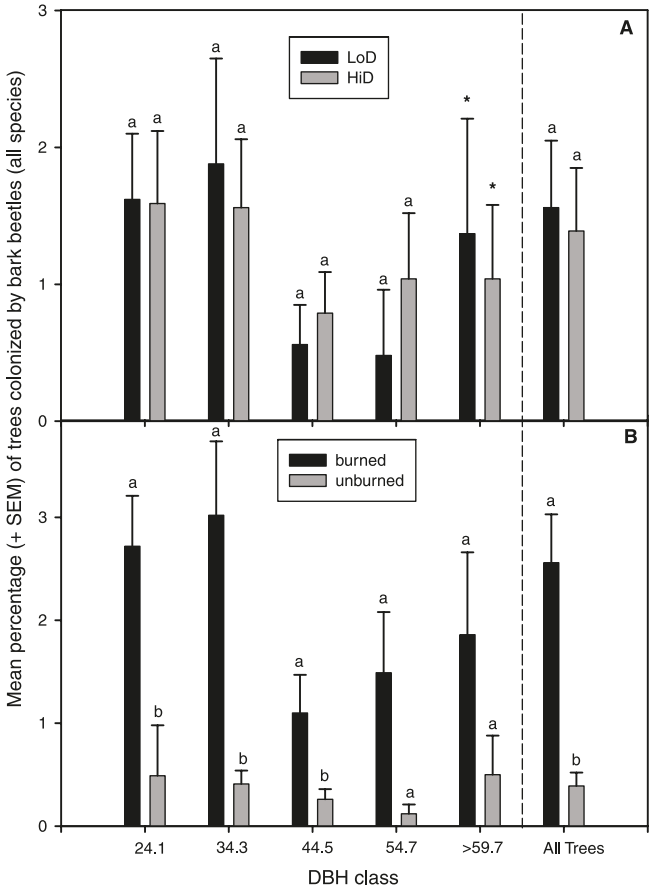
companied by those of other bark beetles within the same tree. Accordingly, in reference to WPB, MPB, JPB, and FE, we attributed tree mortality to one of these species if evidence of colonization was found despite the potential existence of other bark beetle species. On occasion (12 trees), we found WPB and MPB infesting the same tree. In these situations, we attributed tree mortality to WPB. Tree mortality was attributed to *Ips* spp. only when evidence of WPB, MPB, or JPB colonization was absent. Mortality was only attributed to WPB, MPB, JPB, FE, and *Ips* when burn severity rankings on individual trees were ≤3 (i.e., we estimated that prescribed fire did not directly kill the tree based on external measures of fire severity; Fettig et al. 2002). *Hylastes* spp., primarily *Hylastes macer* LeConte, *Hylurgops* spp., primarily *Hylurgops subcostulatus* (Mannerheim) (80 trees combined), and *Pseudohylesinus* spp. (20 trees) were occasionally found colonizing trees that had been attacked by other bark beetles or heavily injured by prescribed burns. These species are generally not considered tree killers (Furniss and Carolin 1977). Presence of *Hylastes*, *Hylurgops*, and *Pseudohylesinus* spp. was noted, but no other analyses were conducted.

We also found RTB, a common bark beetle species found throughout much of North America, colonizing many trees. RTB attacks are usually confined to basal portions of previously stressed, weakened, or dead and dying trees (Furniss and Carolin 1977) or those under attack by other bark beetles, such as WPB (Hall 1983; Fettig et al. 2004). Attacks are typically not considered to be a significant threat to tree health. However, tree mortality was attributed to RTB in a 17-year-old ponderosa pine plantation in northern California (Rappaport et al. 2001), in several trees in stands where logging residues were chipped and retained on-site in northern California (Fettig et al. 2006), and in *Pinus tabuliformis* Carrière forests in China where RTB was accidentally introduced (Li et al. 2001). In addition, accuracy of logistic regression models for predicting probability of ponderosa and Jeffrey pine mortality following mixed-severity wildfire was increased when presence of RTB attacks was included (Hood et al. 2007). Despite this, we did not attribute tree mortality to RTB attacks in this study.

Among all plots, a total of 2733 pine and fir trees (1.5% of all trees) were colonized by bark beetles (all species), of which 46% (1256 trees) occurred on LoD treatments (Fig. 3A). Overall, no significant difference in the mean percentage of trees killed by bark beetles was found between treatments or within individual diameter classes (Fig. 3A). The application of prescribed fire resulted in a significant increase in bark beetle caused tree mortality overall ($F_{[1,16]} = 78.6$, $P < 0.0001$) (Fig. 3B) and within individual diameter classes ($P < 0.03$, all cases) (Fig. 3B), except the two largest classes (Fig. 3B). Approximately 85.6% (2339 trees) of all bark beetle caused tree mortality occurred on burned split plots. Bark beetles are considered important mortality agents following prescribed fires and mixed-severity wildfires in coniferous forests (reviewed in Parker et al. 2006).

Bark beetle caused tree mortality accounted for 28.8% of total tree mortality (2733 of 9500 trees by all causes) with the remainder primarily attributed to fire effects. A limitation of our experimental design is that it did not permit a statistically valid comparison with an untreated control

Fig. 3. Mean percentage of trees colonized by bark beetles (all species combined) by diameter class (midpoint of 10 cm diameter classes shown except for the largest diameter class) and for all trees by (A) forest structure (LoD, low diversity; HiD, high diversity) and (B) application of prescribed fire (with and without), Blacks Mountain Experimental Forest, California. Means (+SEM) with the same letter within groups are not significantly different ($P > 0.05$). Asterisks denote that analyses were not conducted.



(Oliver 2000). However, two adjacent RNAs provided an estimate of background levels of bark beetle caused tree mortality at BMEF during this period. The percentage of trees killed by bark beetles (all species) on RNA-A (34 ha) and RNA-C (51 ha) was 1.35% and 3.29%, respectively. The much higher levels of bark beetle caused tree mortality in RNA-C are attributed to the application of prescribed fire in that unit.

Western pine beetle

Overall, the number of trees killed by WPB (442 trees) and MPB (468 trees) were similar (Figs. 4 and 5). Less than 0.6 and 0.9 tree/ha was killed by these two species combined on LoD and HiD, respectively. While SDI relationships described by Oliver (1995) are a tenuous fit for the HiD treatment, which does not represent an even-aged structure, it is quite appropriate for the LoD treatment. LoD plots averaged SDI values of 118 and 124 for the unburned and burned split plots, respectively. These values are much less than the *Dendroctonus* limiting maximum SDI value of 365 previously described for stands in northern California or 230, which defines a threshold for a zone of imminent

Fig. 4. Mean percentage of ponderosa pine colonized by western pine beetle by diameter class (midpoint of 10 cm diameter classes shown except for the largest diameter class) and for all trees by (A) forest structure (LoD, low diversity; HiD, high diversity) and (B) application of prescribed fire (with and without), Blacks Mountain Experimental Forest, California. Means (+SEM) with the same letter within groups are not significantly different ($P > 0.05$). Asterisks denote that analyses were not conducted.

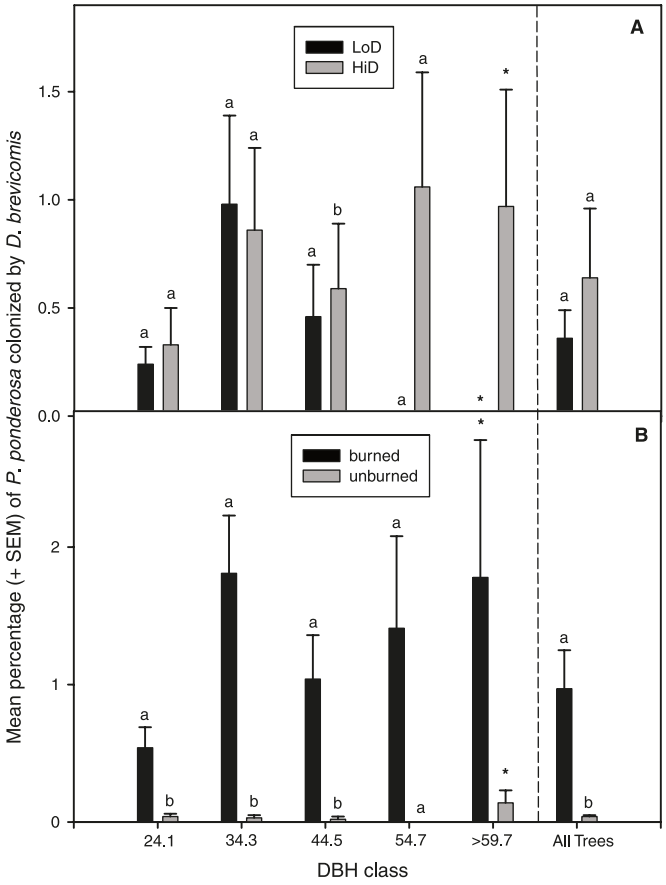
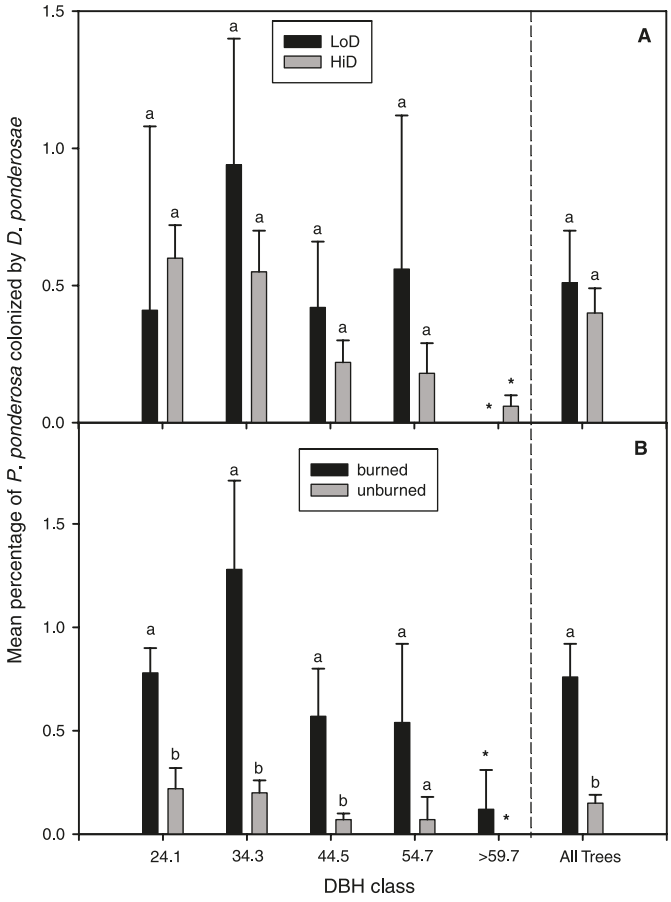


Fig. 5. Mean percentage of ponderosa pine colonized by mountain pine beetle by diameter class (midpoint of 10 cm diameter classes shown except for the largest diameter class) and for all trees by (A) forest structure (LoD, low diversity; HiD, high diversity) and (B) application of prescribed fire (with and without), Blacks Mountain Experimental Forest, California. Means (+SEM) with the same letter within groups are not significantly different ($P > 0.05$). Asterisks denote that analyses were not conducted.



WPB- and MPB-caused tree mortality (Oliver 1995). Similarly, residual stand densities for both treatments are much lower than the threshold value of 34.4 m^2/ha basal area reported by Sartwell and Stevens (1975) above which stands are more susceptible to MPB infestation.

Among all plots, 0.4% of ponderosa pines were killed by WPB, of which 31.4% (139 trees) occurred on LoD treatments (Fig. 4A). Ponderosa pine is the only host of WPB present in these stands (Miller and Keen 1960). Overall, no significant difference in the mean percentage of trees killed by WPB was found between treatments or within most individual diameter classes (Fig. 4A); however, significantly higher levels of WPB-caused tree mortality occurred on HiD plots in the 44.5 cm diameter class ($F_{[1,2]} = 69.8$, $P = 0.01$). No WPB-caused tree mortality was found within LoD plots in the two largest diameter classes (Fig. 4A), which is surprising given the beetle's preference for larger diameter trees (50.8–81.3 cm DBH; Person 1928; Miller and Keen 1960) and may be an artifact of only 359 and 30 trees occurring within the 54.7 and 59.7 cm diameter classes on LoD plots, respectively. This represents an average density of <0.7 ponderosa pine >39.4 cm DBH/ha.

The application of prescribed fire resulted in a significant increase in WPB-caused tree mortality overall ($F_{[1,16]} = 49.9$, $P < 0.0001$) (Fig. 4B) and within individual diameter classes ($P < 0.003$, all cases) (Fig. 4B), except the 54.7 and >59.7 cm diameter classes (data not analyzed) (Fig. 4B). Approximately 96.2% (425 trees) of all WPB-caused tree mortality occurred on burned split plots. McHugh et al. (2003) reported that WPB colonized only three of 222 trees following a prescribed fire on the Coconino National Forest in Arizona. However, mortality in fire-damaged ponderosa pine as a result of attacks by WPB has been previously reported (Miller and Patterson 1927; Miller and Keen 1960).

Mountain pine beetle

Among all plots, 0.4% of all ponderosa pines were killed by MPB, of which 49.1% (230 trees) occurred on LoD treatments (Fig. 5A). Although MPB colonizes several hosts (Furniss and Carolin 1977), it was only found colonizing ponderosa pine at BMEF, as few other hosts were present. Overall, no significant difference in the mean percentage of trees killed by MPB was found between treatments or within

individual diameter classes (Fig. 5A). Fiddler et al. (1989) showed that thinning significantly reduced the amount of ponderosa pine mortality caused by MPB in northeastern California. No tree mortality occurred in stands of <9 m^2/ha basal area, which agrees with the optimal stocking level of 11 m^2/ha described by Oliver (1979, 1995). The application of prescribed fire resulted in a significant increase in MPB-caused tree mortality overall ($F_{[1,16]}$ = 31.7, $P < 0.0001$) (Fig. 5B) and within individual diameter classes ($P < 0.005$, all cases) (Fig. 5B), except the 54.7 and >59.7 cm diameter classes (data not analyzed) (Fig. 5B). Approximately 83.3% (390 trees) of all MPB-caused tree mortality occurred on burned split plots.

Jeffrey pine beetle

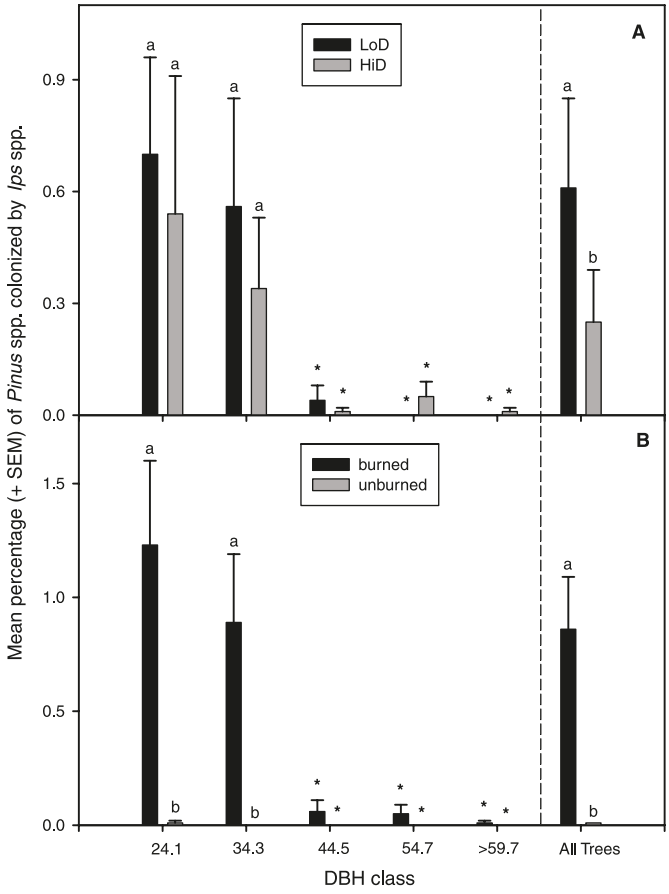
A total of 18 Jeffrey pines (0.1% of all Jeffrey pine) were colonized by JPB, and therefore, statistical analyses were not conducted. Approximately 89% (16 trees) of JPB-colonized trees occurred on burned split plots. Bradley and Tueller (2001) investigated effects of low-intensity, late-season prescribed fire on Jeffrey pine and associated short-term responses of bark beetles (several species) in the Lake Tahoe Basin, California. A highly significant correlation was found between prescribed burning and bark beetle infestation, but JPB colonized few trees (19 of 389).

Ips spp.

A total of 494 pines (0.4% of all pines) were colonized by *Ips* spp., of which 69% (341 trees) occurred on LoD treatments. This is likely influenced by a higher proportion of susceptible hosts (i.e., smaller diameter trees) present on LoD treatments (Fig. 1). PE is reported to most frequently colonize trees 5–20 cm DBH (Furniss and Carolin 1977; Kegley et al. 1997), and attack rates are negatively correlated with tree DBH in ponderosa pine (Kolb et al. 2006). While concerns regarding population increases in slash and subsequent colonization of residual leave trees are important, harvest criteria at BMEF required utilization (i.e., biomass or chips) and removal of slash resulting from thinning (Oliver 2000). This likely had an impact in limiting *Ips* attacks on residual trees (Fellin 1980; Parker 1991; Kegley et al. 1997). Overall, significantly more *Ips*-caused tree mortality occurred on LoD versus HiD treatments ($F_{[1,2]}$ = 21.4, P = 0.04). No significant differences were found within individual diameter classes (Fig. 6A). Few *Ips*-killed trees (five trees) occurred in the three largest diameter classes, and therefore, statistical analyses were not conducted (Fig. 6A).

The application of prescribed fire resulted in a significant increase in the proportion of pines killed by *Ips* spp. overall ($F_{[1,16]}$ = 61.5, $P < 0.0001$) (Fig. 6B) and within the two smallest diameter classes ($P < 0.0002$, both cases) (Fig. 6B). Approximately 99.4% (491 trees) of all *Ips*-caused tree mortality occurred on burned split plots. Bradley and Tueller (2001) reported that 36 of 389 pines were colonized by *Ips* spp. the year following prescribed burns in the Lake Tahoe Basin. Ganz et al. (2003) studied effects of prescribed fire on susceptibility of ponderosa and Jeffrey pines to bark beetle attack in two case studies in stands similar to BMEF. Between sites, >30% of pines (98 trees) were killed by PE the first year following prescribed burns.

Fig. 6. Mean percentage of pines colonized exclusively by *Ips* spp. by diameter class (midpoint of 10 cm diameter classes shown except for the largest diameter class) and for all trees by (A) forest structure (LoD, low diversity; HiD, high diversity) and (B) application of prescribed fire (with and without), Blacks Mountain Experimental Forest, California. Means (+SEM) with the same letter within groups are not significantly different ($P > 0.05$). Asterisks denote that analyses were not conducted.



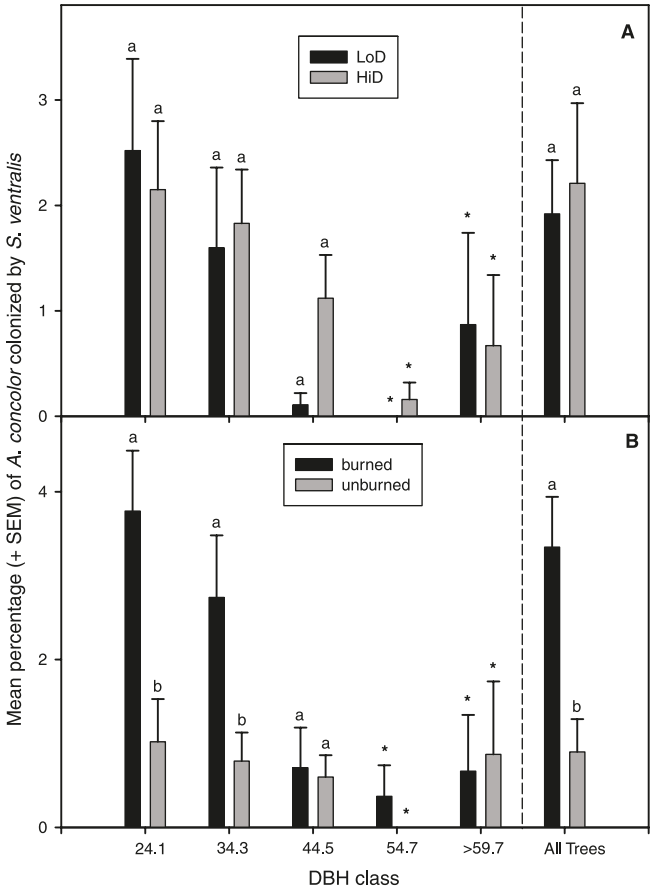
Fir engraver

A total of 1300 white fir (2.0% of all white fir) were colonized by FE, of which 41.3% (537 trees) occurred on LoD treatments. Overall, no significant difference in the mean percentage of trees killed by FE was found between treatments or within individual diameter classes (Fig. 7A). Few trees (seven trees) occurred in the two largest diameter classes, and therefore, statistical analyses were not conducted (Fig. 7A). The application of prescribed fire resulted in a significant increase in the proportion of white fir colonized by FE overall ($F_{[1,13]}$ = 30.0, $P < 0.0001$) (Fig. 7B) and within the two smallest diameter classes ($P < 0.007$, both cases) (Fig. 7B). Similarly, Schwilk et al. (2006) reported that the probability of FE attack and associated levels of tree mortality were greater for smaller diameter firs following prescribed fire in the central Sierra Nevada. Approximately 77.5% (1007 trees) of all FE-caused tree mortality occurred on burned split plots in our study.

Red turpentine beetle

Overall, we found no significant difference between treat-

Fig. 7. Mean percentage of white fir colonized by fir engraver by diameter class (midpoint of 10 cm diameter classes shown except for the largest diameter class) and for all trees by (A) forest structure (LoD, low diversity; HiD, high diversity) and (B) application of prescribed fire (with and without), Blacks Mountain Experimental Forest, California. Means (+SEM) with the same letter within groups are not significantly different ($P > 0.05$). Asterisks denote that analyses were not conducted.



ments with regard to the percentage of dead pines (all sources) colonized by RTB or the mean number of attacks per tree (4.43 ± 0.45 and 7.15 ± 0.88 attacks in LoD and HiD, respectively). The application of prescribed fire resulted in a significant increase in the proportion of pines colonized by RTB ($F_{[1,16]} = 7.85$, $P < 0.01$), but no significant differences were observed within individual diameter classes. Approximately 72.7% of all dead pines in burned split plots contained RTB attacks. Trees averaged 5.16 ± 0.11 and 6.47 ± 0.80 attacks per tree in burned and unburned split plots, respectively ($F_{[1,16]} = 6.88$, $P < 0.02$). The lower attack rate on burned split plots results from many pines containing only one or two attacks, while few such trees occurred on unburned split plots.

In recent years, RTB infestations appear to be increasing throughout the Pacific Northwest (Fettig et al. 2004), and with a greater emphasis on the use of prescribed fire as a management tool, this trend will likely increase (Ferrell 1996; Ganz et al. 2003). In this study, we catalogued 53 trees that had ≥30 RTB attacks per tree, of which 96.2% (51 trees) occurred on burned split plots. Overall, 98.4% (4182 trees) of all pines that were attacked by RTB occurred on burned split plots, including four trees that had >90 RTB attacks per tree. There is a potential for RTB populations to increase in fire-injured pines and attack residual apparently healthy trees. The negative effects of prolonged and large numbers of RTB attacks on residual live trees (not reported here) may not be realized for some time.

Wood borers

Trees that are colonized by primary bark beetles (e.g., WPB or MPB) are often subsequently infested by wood borers. However, trees directly killed by prescribed fire are generally infested by wood borers, but not primary bark beetles (Parker et al. 2006). In our study, of 4556 dead trees with currently fading crowns (i.e., lime or yellow in color) sampled for insect colonization, 3.3% (152 trees) had evidence of primary bark beetles only, which is likely an artifact of time since colonization, as many of these trees were just beginning to fade. To that end, it is likely that these trees will be subsequently colonized by wood borers. Forty percent (1822 trees) had evidence of wood borer attacks only, and 56.7% (2582 trees) were colonized by both groups, which is the most common condition (C.J. Fettig, unpublished data).

Some wood borers are attracted to fires (Evans 1966), smoke (Gardiner 1957; Wickman 1964), and fire-injured trees (Rasmussen et al. 1996), but their contribution to tree mortality, while thought to be rare (Mitchell and Martin 1980; DeNitto et al. 2000; Parker et al. 2006), is largely unknown (Rasmussen et al. 1996). Several species are regarded as forest pests (Furniss and Carolin 1977). For example, California flatheaded borer, *Melanophila californica* Van Dyke, and flatheaded fir borer, *Melanophila drummondi* (Kirby), are known to cause tree mortality, particularly during extended periods of drought (Furniss and Carolin 1977). In Montana, fire-weakened Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and western larch, *Larix occidentalis* Nutt., were killed by flatheaded fir borer up to 1 year after the fire event (K. Gibson, USDA Forest Service, personal communication). Several species of wood borers (*Monochamus* spp.) are also known vectors of a wilting disease caused by pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickel (Linit 1988). While wood borers may not be considered an important source of tree mortality, lumber degrade and introduction of wood decay fungi may be of concern if salvage is planned.

In our study, the percentage of dead trees that were attacked by bark beetles and (or) wood borers (4556 trees) that contained wood borers only (i.e., presence of primary bark beetles was not evident) was significantly higher in burned than in unburned split plots (39.1 ± 5.7% and 5.5 ± 4.0%, respectively; $F_{[1,16]} = 36.22$, $P < 0.001$). Analyses were limited to data where the tree crown was actively fading (i.e., lime or yellow in color), suggesting that tree mortality, as indicated by presence of crown fade, had occurred during the second year following prescribed burns. Data suggest that wood borers are directly contributing to tree mortality in fire-injured trees at BMEF, as this mortality likely would not have occurred in the absence of wood borer attacks (i.e., these trees were green the summer following prescribed burns) in the near-term. McHugh et al. (2003) found that wood borers were the most common insect found in trees

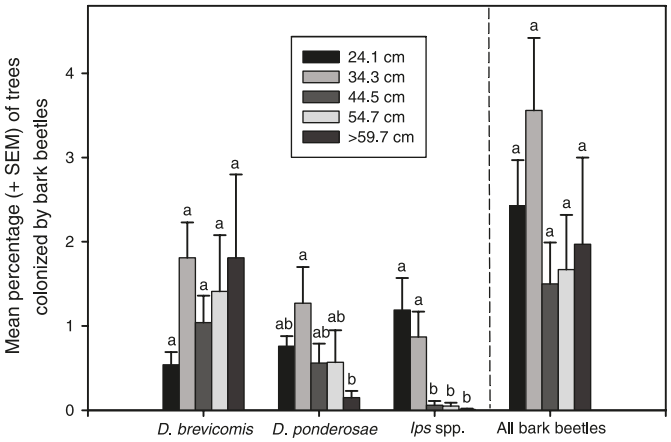
following mixed-severity wildfires and prescribed fires in ponderosa pine stands in northern Arizona. In their study, colonization primarily occurred the first year following burns.

Management implications

One of the primary objectives of the BMEF study was to create stand conditions that serve as a model of resiliency to allogenic (e.g., wildfire) and autogenic (e.g., bark beetle infestations) disturbances. To that end, concerns about maintaining large-diameter pines, particularly on HiD, were expressed among the interdisciplinary team. Generally, larger trees are more fire resistant (Peterson and Ryan 1986; Harrington 1993; Thies et al. 2005) but may be 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 intensity and fine-root injury. Larger trees may also be less vigorous than smaller trees, reducing their capability to recover from fire-associated injuries (McHugh and Kolb 2003). Several studies have reported that bark beetle colonization rates are positively correlated with tree diameter in ponderosa pine (Fettig et al. 2007), but we found no significant differences in the proportion of pines killed by bark beetles (all species) among diameter classes, and for WPB specifically, on burned split plots (Fig. 8). However, 6% of ponderosa pines >59.7 cm DBH died as a result of WPB attack on experimental unit 49. Both MPB and *Ips* spp. colonized larger diameter trees less frequently (Fig. 8). In the near-term (2 years postburn), concerns regarding delayed mortality of large-diameter ponderosa and Jeffrey pines at BMEF following restoration treatments seem unfounded. However, this relationship could change in the future, particularly if significant root damage has occurred as a result of the application of prescribed fire.

Several studies have explored the effects of silvicultural treatments on bark beetle acitivity, but most are limited to investigations conducted on small plots usually ≤4 ha in size that may not reflect reasonable management scenarios and could confound results (Schmid and Mata 2005). Our study was conducted at a larger spatial scale than previously reported in the scientific literature (Table 2). Among all plots, a total of 9500 (5.0% of all trees) pine and fir trees died following treatment, of which 28.8% (2733 trees) was attributed to bark beetle colonization. This relatively low rate of bark beetle caused tree mortality is not surprising given the residual stand densities achieved in this study (Sartwell and Stevens 1975; Oliver 1995; Fettig et al. 2007). Overall, we observed no significant differences in tree mortality, bark beetle caused tree mortality (all bark beetle species), and WPB-, MPB-, and FE-caused tree mortality between LoD and HiD stand structures. We observed significantly higher levels of *Ips*-caused tree mortality in the LoD treatment, most of which occurred in the smaller diameter classes. These results suggest that LoD and HiD stand structures at BMEF are of similar resilience to bark beetle infestations. However, we emphasize that these results pertain to short-term responses under certain abiotic and bark beetle population pressures. At the beginning of this study, tree mortality attributed to WPB, MPB, JPB, and FE in northeastern California declined to what was considered "background levels" (USDA Forest Service 1997–2002) following an earlier period of elevated activity. In 2001, activity of these species, with the exception of JPB, began to increase in portions of northeastern California (USDA Forest Service 1997–2002). A more significant test of the resiliency of these treatments and resulting structures will occur if bark beetle populations continue to build in the region.

Fig. 8. Colonization rates of available pines among diameter classes (midpoint of 10 cm diameter classes shown except for the largest diameter class) on burned split plots for western pine beetle, mountain pine beetle, *Ips* spp., and all bark beetle species, Blacks Mountain Experimental Forest, California. Means (+SEM) with the same letter within groups are not significantly different ($P > 0.05$).



We conclude that near-term levels of bark beetle caused tree mortality (1.5% of all trees) do not interfere with management objectives, particularly considering that almost half (47.6%) is represented by FE infesting white fir, as treatments were designed to promote ponderosa and Jeffrey pines over white fir (Oliver 2000). We issue one caveat that the effects of RTB attacks and prescribed fire on individual tree health and subsequent levels of tree mortality may not be realized for some time. We intend to continue monitoring these experimental units for bark beetle responses in the future and determine the longer-term effects of these treatments and resulting stand structures on the amount of bark beetle caused tree mortality.

Acknowledgments

We thank D. Meyers and E. Koenigs (formerly Pacific Southwest Research Station), L. Patterson (University of Nevada-Reno), A. Piscitelli (Humboldt State University), and C. Mautner (University of California-Berkeley) for technical assistance and acknowledge the numerous contributions of B. Oliver and M. Ritchie (Redding Silvicultural Laboratory, Pacific Southwest Research Station) and the Lassen National Forest without which this study would not have been possible. We also thank our numerous colleagues on the Blacks Mountain Experimental Forest Ecological Research Team for their participation in this large-scale study and P. Shea (formerly Pacific Southwest Research Station) for his support of this research. Sylvia Mori (Pacific Southwest Research Station) provided advice and input on statistical analyses. Special thanks to K. Gibson (Forest Health Protection, USDA Forest Service) and two anonymous reviewers for their critiques, which greatly

improved earlier versions of this manuscript. This research was supported, in part, by ecosystem management research funds received through the Washington Office of the USDA Forest Service and the Pacific Southwest Research Station. This article was written and prepared by US Government employees on official time and it is, therefore, in the public domain and not subject to copyright.

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