

RESEARCH ARTICLE

BARK BEETLE RESPONSES TO STAND STRUCTURE AND PRESCRIBED FIRE AT BLACKS MOUNTAIN EXPERIMENTAL FOREST, CALIFORNIA, USA: 5-YEAR DATA

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ABSTRACT

Highly effective fire suppression and selective harvesting of large-diameter, fire-tolerant tree species, such as ponderosa pine (*Pinus ponderosa* C. Lawson) and Jeffrey pine (*P. jeffreyi* Balf.), have resulted in substantial changes to the structure and composition of interior ponderosa pine forests. Mechanical thinning and the application of prescribed fire are now commonly used to reduce fuel loads and restore late-seral conditions in interior ponderosa pine forests, but the propensity for some bark beetles (Coleoptera: Curculionidae, Scolytinae) to attack fire-injured trees has led to questions regarding how management objectives may be impacted by levels of delayed tree mortality attributed to bark beetle attack. In this study, we examined bark beetle responses to creation of mid-seral (low structural diversity; LoD) and late-seral (high structural diversity; HiD) forest structures at Blacks Mountain Experimental Forest, California, USA, during a five-year period following the application of prescribed fire (B). Twelve experimental plots (LoD and HiD), ranging in size from 77 ha to 144 ha, were split with one half randomly assigned prescribed fire, resulting in four treatments (HiD, HiD + B, LoD, and LoD + B). A total of 6877 pine and fir (*Abies*) trees (4.0% of all trees) were killed by bark beetles (all bark beetle species combined). Most of the tree mortality was attributed to western pine beetle (*Dendroctonus brevicomis* LeConte) and mountain pine beetle (*D. ponderosae* Hopkins) in ponderosa pine, and fir engraver (*Scolytus ventralis* LeConte) in white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.). The majority of bark beetle-caused tree mortality was recorded on HiD + B (41.5% of trees that were killed by bark beetles) with 30.0%, 23.5%, and 5.0% occurring on HiD, LoD + B, and LoD, respectively. Overall, a significantly higher percentage of bark beetle-caused tree mortality (of available trees) occurred on LoD + B (5.3%) and HiD + B (4.8%) compared to LoD (1.1%). We observed no significant differences in levels of bark beetle-caused tree mortality (all bark beetle species combined) among diameter classes, but the level of western pine beetle-caused tree mortality was concentrated in the large tree component on burned split plots, which differs from results obtained two years after the application of prescribed fire. The amount of bark beetle-caused tree mortality increased substantially on unburned split plots compared to burned split plots following our initial survey (i.e., three years to five years after the application of prescribed fire). The implications of these and other results for the management and maintenance of late-seral conditions in interior ponderosa pine forests are discussed.

Keywords: *Abies concolor*, *Dendroctonus*, fuel reduction, *Ips*, *Pinus jeffreyi*, *Pinus ponderosa*, resiliency, *Scolytus*

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INTRODUCTION

Prior to Euro-American settlement, the interior ponderosa pine (*Pinus ponderosa* C. Lawson var. *ponderosa*) forest type in California, USA, was dominated by open and park-like stands of widely dispersed ponderosa and Jeffrey pines (*P. jeffreyi* Balf.), particularly on xeric sites. Frequent thinning of small-diameter (<19 cm diameter at breast height [dbh]) 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). Today, many of these forests are denser, have more small trees and fewer large trees, and are dominated by more shade tolerant and fire intolerant tree species, such as white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.). These conditions are primarily a result of fire exclusion and past harvesting practices, and have led to heavy accumulations of surface and ladder fuels (Youngblood *et al.* 2004).

Large and severe wildfires in the western USA, particularly in California, have aroused public concern and manifested the need for well designed silvicultural treatments to reduce their extent and severity. Creating more fire resilient stands generally requires treatment of surface and ladder fuels, reductions in crown density, and maintenance of large diameter trees (Agee and Skinner 2005). A combination of thinning and prescribed fire has been shown to be highly effective for reducing the severity of wildfires in interior ponderosa pine forests. For example, Ritchie *et al.* (2007) studied the effects of fuel reduction treatments (including those detailed in this study) at Blacks Moun-

tain Experimental Forest (BMEF), California, USA, on fire severity at the point of transition between treated and untreated stands that were later impacted by a wildfire. Tree survival was highest in areas that were both thinned and prescribed-burned. Survival in thinned-only areas was significantly greater than in untreated areas, but less than in areas that had received the combined thinned and prescribed-burned treatment (Ritchie *et al.* 2007).

Mechanical fuel treatments and the application of prescribed fire may also influence the amount and distribution of bark beetle- (Coleoptera: Curculionidae, Scolytinae) caused tree mortality at various spatial and temporal scales. For example, treatments may affect the health and vigor of residual trees; the size, distribution, and abundance of preferred hosts; and the physical environment within forest stands (Fettig *et al.* 2007). Carelessly implemented treatments may result in physical damage to residual trees, soil compaction, and increased rates of windthrow, increasing the likelihood of tree colonization by bark beetles, other subcortical insects, and root pathogens (Schweigkofler *et al.* 2005). Furthermore, tree volatiles released during harvest operations, including monoterpenes, are known to influence the physiology and behavior of bark beetles (Seybold *et al.* 2006) and colonization rates of trees by bark beetles in ponderosa pine forests (Fettig *et al.* 2006).

Forest health professionals have recognized that stand susceptibility to bark beetle attack can be manipulated by addressing factors related to tree density (Fettig *et al.* 2007), typically through mechanical thinning. For example, Sartwell (1971) presented data on radial growth and its relationship to mountain

pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) attack and suggested that slow growth was characteristic of nearly all pines killed by MPB in the Pacific northwest, USA. The author concluded that thinning to reduce tree competition and increase individual tree growth was critical to reducing stand susceptibility to bark beetle attack. Oliver (1995) reported maximum stand density index (SDI) for even-aged ponderosa pine stands in northern California was regulated by MPB and western pine beetle (WPB; *Dendroctonus brevicomis* LeConte) infestations. An SDI value of 230 defined a threshold for a zone of bark beetle-caused tree mortality within which endemic populations kill a few trees but net growth is positive. Maximum SDI was defined at 365. More recently, Hayes *et al.* (2009) suggested lower SDI thresholds based on models constructed from 44 stands throughout California. Fettig *et al.* (2007) discussed tree and stand factors associated with bark beetle infestations in ponderosa pine forests, and provided mechanistic explanations on the effectiveness of reducing stand density for preventing bark beetle infestations.

Bark beetles may attack and kill trees that were injured by fire but might have otherwise survived (Parker *et al.* 2006, Jenkins *et al.* 2008). These trees may then serve as a source of beetles and attractive semiochemicals (e.g., host volatiles and aggregation pheromones produced by many bark beetle species during host colonization) that attract other beetles into the vicinity, resulting in additional levels of tree mortality. The propensity for many species of bark beetles to attack fire-injured trees has led to questions regarding how the amount and distribution of bark beetle-caused tree mortality may be affected by the application of fuel reduction treatments. Maintenance of large trees, an important component of late-seral stands, is of primary concern. Kolb *et al.* (2007) suggested that growth of large ponderosa pines can be accelerated by thinning, but warned that prescribed fire may predispose

trees to increased levels of delayed mortality, often caused by bark beetle attack. Recent work at BMEF showed increased vigor in thinned stands, but also an increase in mortality of large trees when thinning was followed by prescribed fire (Ritchie *et al.* 2008). However, the authors suggested that this is likely a one-time phenomenon occurring shortly after the application of prescribed fire.

In recent years, a substantial body of work has been published documenting the ecological effects of fuel reduction and forest restoration treatments in ponderosa pine forests. Most efforts have quantified short-term (<5 yr) responses obtained from small-scale (<10 ha) experimental plots. In the mid-1990s, an interdisciplinary team of scientists was formed at BMEF to conduct long-term ecological research designed “to increase our understanding of the effect of forest structural complexity on the health and vigor of an interior ponderosa pine ecosystem; to quantify the ecosystem’s responses to natural and human-induced disturbance; and to determine how these ecosystems can be restored and managed” (Oliver 2000). Our work is part of the resulting research project (Blacks Mountain Ecological Research Project) managed by the Pacific Southwest Research Station of the Forest Service and conducted at large spatial scales that represent reasonable management scenarios in these forests. The initial responses of vegetation (Ritchie *et al.* 2008, Zhang *et al.* 2008), invertebrates (Camann *et al.* 2008, Fettig *et al.* 2008, Gillette *et al.* 2008), and birds and small mammals (George and Zack 2008, Maguire *et al.* 2008) to treatments at BMEF have been described. An earlier publication (Fettig *et al.* 2008) described short-term responses of bark beetles captured during our initial survey conducted two years after the application of prescribed fire at BMEF, in which we reported that prescribed burns resulted in significant increases in the amount of bark beetle-caused tree mortality (all bark beetle species combined) and for WPB, MPB, and fir engraver

(FE, *Scolytus ventralis* LeConte) individually. Our objectives for this study are to document the responses of bark beetles during a five-year period after the application of prescribed fire, and to compare trends in levels of tree mortality attributed to bark beetle attack between the two surveys.

METHODS

Study Site and Treatment

We conducted this study at Blacks Mountain Experimental Forest (BMEF; 40°40' N, 121°10' W; 1700 m to 2100 m elevation) located on the Lassen National Forest, California, USA. The climate at BMEF is characterized by hot, dry summers and cold, moist winters. Mean daily temperatures range from -9°C to 29°C. The growing season is about 120 days. Annual precipitation averages 50.8 cm with most falling as snow between October and May. The overstory at BMEF is dominated by ponderosa pine with varying amounts of white fir, incense cedar (*Calocedrus decurrens* [Torr.] Florin) and Jeffrey pine, depending on elevation and aspect. Prior to treatment, stands were dominated by two age cohorts consisting of 300 yr to 500 yr old pines and incense cedars, and a dense understory and mid-story of 50 yr to 100 yr old pines, white firs, and incense cedars (Oliver and Powers 1998, Zhang *et al.* 2008).

We established twelve experimental plots, ranging in size from 77 ha to 144 ha, to create two distinct forest structural types: mid-seral stage (low structural diversity; LoD) and late-seral stage (high structural diversity; HiD). We randomly assigned structures to four experimental plots (two replicates per structure per block) within each of three blocks. Blocking allowed us to allocate variation to differences in tree species composition associated with elevation gradients and year of treatment. We created LoD by removing larger overstory trees and small understory trees, leaving only

trees of intermediate size. We created HiD by thinning smaller trees and retaining larger trees (i.e., thinning from below). Following harvesting, we treated half of each plot with prescribed fire in fall (Table 1). Fettig *et al.* (2008) describe in detail the climatic conditions, fuel moistures, and other parameters that occurred during prescribed burns (Table 2). The BMEF is included in grazing allotments; therefore, we fenced 6 of 12 experimental plots in an attempt to exclude grazing and permit analyses of the effect of grazing on several variables of interest to the interdisciplinary team. We viewed grazing as having little or no influence on bark beetle activity (Fettig *et al.* 2008) and was ignored in our analyses. Furthermore, grazing was inconsistent (i.e., concentrated in areas around water) and some cattle gained access to ungrazed plots. Oliver (2000) and Zhang *et al.* (2008) provide a comprehensive account of treatments. Prior to treatment, the average stand density of proposed experimental units was $32.4 \text{ m}^2 \text{ ha}^{-1} \pm 1.5 \text{ m}^2 \text{ ha}^{-1}$ (SEM) of basal area. There were $871 \text{ trees ha}^{-1} \pm 58 \text{ trees ha}^{-1}$ (SEM) composed of 57% ponderosa and Jeffrey pines and 36% white fir (Zhang *et al.* 2008). Immediately following treatment, average values for LoD and HiD were $\sim 10 \text{ m}^2 \text{ ha}^{-1}$ and $25 \text{ m}^2 \text{ ha}^{-1}$ of basal area, and $282 \text{ trees ha}^{-1}$ and $513 \text{ trees ha}^{-1}$, respectively. Species composition ranged from 49% ponderosa and Jeffrey pines and 42% white fir (HiD + B), to 61% ponderosa and Jeffrey pines and 29% white fir (LoD + B) (Zhang *et al.* 2008).

Data Collection and Analyses

We conducted a 100% cruise (census) on each experimental plot to locate dead and dying pine and fir trees by presence of crown fade, an irreversible symptom of tree mortality. Because both incense cedar and western juniper (*Juniperus occidentalis* Hook.) are minor components of BMEF (i.e., representing <7.7% and <0.1% of trees, respectively), these

Table 1. Evaluation dates, Blacks Mountain Experimental Forest, California, USA.

Plot	Structure ^a	Prescribed burn (mo/yr)	Initial survey ^b (mo/yr)		Second survey ^c (mo/yr)
			Unburned	Burned	All
38	HiD	10/1997	9/1998	8/1999	9/2002
39	LoD	10/1997	9/1998	9/1999	9/2002
40	LoD	10/2000	8/2002	7/2002	8/2005
41	HiD	10/1997	8/1998	8/1999	9/2002
42	HiD	11/1999	9/2001	8/2001	9/2004
43	LoD	10/1997	8/1998	8/1999	10/2002
44	LoD	11/1999	7/2001	8/2001	8/2004
45	LoD	11/1999	10/2001	10/2001	10/2004
46	LoD	10/2000	6/2002	6/2002	^d
47	HiD	11/1999	7/2002	7/2002	8/2004
48	HiD	10/2000	7/2002	7/2002	8/2005
49	HiD	10/2000	8/2002	8/2002	10/2005

^a HiD = high structural diversity, LoD = low structural diversity (Oliver 2000).

^b Burned split plots were initially cruised the second field season following application of prescribed fire. Generally, this amount of time is sufficient to allow distinction between crown scorch resulting from fire, and crown fade associated with tree mortality attributed to bark beetle attack.

^c All plots were surveyed the fifth field season following the application of prescribed fire.

^d Plot heavily damaged by wildfire and excluded from analyses.

Table 2. Parameters of prescribed burn treatments applied to 12 experimental units at Blacks Mountain Experimental Forest, California, USA.

Variable	Block 1	Block 2	Block 3
Burn parameters			
Date	25 September to 5 October 1997	1 to 4 November 1999	18 to 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 mm to 25 mm	10.5 ± 1.3	18.2 ± 1.1	18.1 ± 1.1
25 mm to 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.

species generally are not attacked and killed by bark beetles and we ignored them. Because of the large spatial scale of this study, we staggered our treatment implementation and our initial (1998 to 2002; Fettig *et al.* 2008) and subsequent (2002 to 2005) surveys across multiple years (Table 1). We identified all recently killed pine and fir trees >19 cm dbh, and tallied and identified the causal agent of mortality. We recorded tree species, dbh, crown color, colonizing bark beetle species, presence of wood borers (Coleoptera: Cerambycidae, Buprestidae), and ranking of burn severity (1 to 4, based on external measures of bole char and bark consumption; Fettig *et al.* 2008, 2010b). We removed a section of bark approximately 625 cm² on each recently killed tree 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 morphology, distribution and orientation of galleries, and the host species are commonly used to distinguish among bark beetle species (Furniss and Carolin 1977). Bark removal also served as a means of separating mortality tallied during the first survey from that of the second survey. Fettig *et al.* (2008) provide a comprehensive description of methods.

On 26 September 2002, a wildfire (Cone Fire) ignited on the Hat Creek Ranger District, Lassen National Forest, USA, adjacent to BMEF and burned portions of 3 of the 12 experimental plots with variable intensities (Ritchie *et al.* 2007). One plot (plot 46) suffered low- to moderate-severity wildfire throughout much of the plot, and therefore was excluded from our analyses. Two other plots were partially burned by the Cone Fire. Only the burned split was impacted in plot 41 and the affected portion (i.e., as noted by the presence of bole char, crown scorch, or both on trees) amounted to about 8.7% (of 55.6 ha). About 27% (of 51.6 ha) of the burned split and 28.2% (of 64.5 ha) of the unburned split were affected in plot 43. We subtracted the affected areas from the original area and adjusted the

composition data accordingly. Cruises for both plots 41 and 43 were originally scheduled for 2002 (i.e., the summer of the wildfire), and were conducted as planned (Table 1).

Our primary variables of interest were the mean percentage of trees killed by 1) all causes, 2) all bark beetle species across all tree species, 3) individual bark beetle and host tree species, and 4) individual bark beetle species by host tree species within diameter class (19 cm to 29.2 cm, 29.3 cm to 39.3 cm, 39.4 cm to 49.5 cm, 49.6 cm to 59.7 cm, and >59.7 cm dbh). The precise role of each bark beetle species in causing tree mortality on our experimental plots is uncertain as fire-damaged trees in interior ponderosa pine forests are susceptible to colonization by several species of bark beetles. In some cases (e.g., WPB), trees must have 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., *Ips* spp.) attacks may occur on dead and dying trees (Furniss and Carolin 1977). Accordingly, in reference to WPB, MPB, Jeffrey pine beetle (JPB; *D. jeffreyi* Hopkins) and FE, we attributed tree mortality to one of these species if evidence of colonization was found despite the potential presence of other bark beetle species. On occasion, we found WPB and MPB infesting the same tree; in these situations, we attributed tree mortality to WPB (Fettig *et al.* 2008). We attributed tree mortality to *Ips* spp. only when evidence of WPB, MPB, or JPB colonization was absent. We attributed mortality to WPB, MPB, JPB, FE, and *Ips* only 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.* 2008). Red turpentine beetle (RTB; *D. valens* LeConte) attacks are typically not considered to be a significant threat to tree health, and therefore, we did not attribute tree mortality to RTB attacks.

We analyzed the data cumulatively over the five-year period (i.e., since the application

of prescribed fire). We used a randomized complete block experimental design with split plots (Oliver 2000) with three blocks, two treatments (HiD and LoD), and two replicates per treatment ($n = 12$). Half of each plot was treated with prescribed fire. Due to the imbalance in the number of plots (i.e., due to the Cone Fire) we used the Satterthwaite approximation method to estimate the appropriate degrees of freedom. We performed an analysis of variance on each response variable at $\alpha = 0.05$ (SAS Institute, Cary, North Carolina, USA). If a significant treatment effect was detected, we used Tukey's multiple comparison test (Tukey's HSD) for separation of treatment means requiring more than one comparison.

RESULTS

During this survey, we examined 173 220 pine and fir trees for mortality and bark beetle activity. Of these, 100 433 (58.0%) were ponderosa pine, 55 396 (32.0%) were white fir, and 17 391 (10.0%) were Jeffrey pine. The number of trees within individual dbh classes (prior to adjustments for the Cone Fire) is reported by Fettig *et al.* (2008).

Overall Tree Mortality

A total of 12 568 (7.3% of all trees) pine and fir trees died during the five-year period, most of which (41.3% of dead trees; 5193 trees) occurred on HiD + B with 37.6%, 18.1%, and 3.0% occurring on LoD + B, HiD, and LoD, respectively. These figures represent mortality attributable to all sources (i.e., fire, bark beetle, mechanical, pathogen, and unidentified sources, and their many interactions). Overall, a significantly higher percentage of tree mortality occurred on LoD + B (15.2% of all trees) than HiD (4.0%) and LoD (1.5%) ($P = 0.003$; Figure 1). In addition, a significantly higher percentage of trees died on HiD + B (9.1%) than LoD. No other significant differences were observed (Figure 1). Treatment ef-

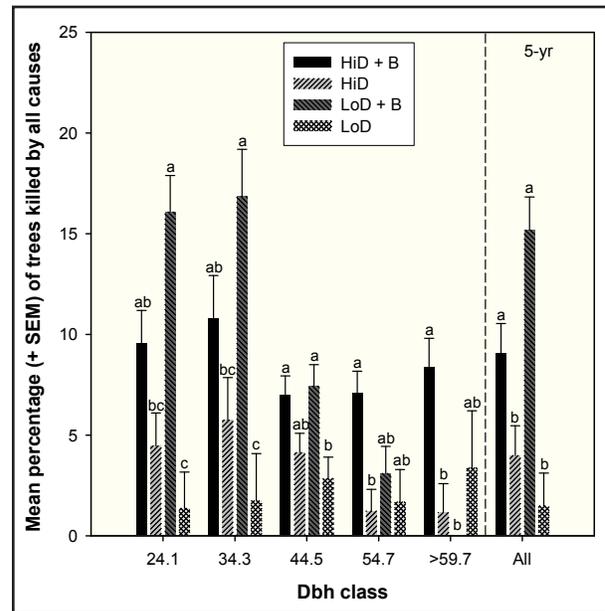


Figure 1. Mean percentage of trees killed by all sources by diameter class (mid-point of 10 cm diameter classes shown except for largest diameter class), and for all trees by treatment (LoD, low structural diversity; HiD, high structural diversity; B, prescribed burn) five years after the application of prescribed fire, Blacks Mountain Experimental Forest, California, USA. Means (+ SE) followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$).

fects varied among dbh classes, but generally the highest levels of mortality were observed in LoD + B ($P < 0.020$, all cases) except in the larger dbh classes (54.7 cm and >59.7 cm) where few large diameter trees occurred (Figure 1). In the 54.7 cm dbh class, a significantly higher percentage of tree mortality occurred on HiD + B (7.1%) than HiD (1.2%) ($P = 0.031$; Figure 1). In the >59.7 cm dbh class, a significantly higher percentage of tree mortality occurred on HiD + B (8.4%) compared to HiD (1.2%) and LoD + B (0%) ($P = 0.024$; Figure 1). Approximately 79% (9916 trees) of all tree mortality occurred on burned split plots, primarily HiD + B.

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 pine engraver (PE, *Ips pini* [Say]) and, to a much lesser extent, emarginate ips (*I. emarginatus* LeConte and *I. latidens* [=*Orthotomicus*] LeConte) colonizing ponderosa and Jeffrey pines. A total of 6877 pine and fir trees (4.0% of all trees) were killed by bark beetles (all bark beetle species combined), the majority of which (41.5% of trees killed by bark beetles; 2857 trees) occurred on HiD + B with 30.0%, 23.5%, and 5.0% occurring on HiD, LoD + B, and LoD, respectively. Overall, a significantly higher percentage of bark beetle-caused tree mortality occurred on LoD + B (5.3% of all trees) and HiD + B (4.8%) than LoD (1.1%) ($P = 0.022$; Figure 2). No other significant differences were observed (Figure 2). Similar effects were observed in the two smallest dbh classes ($P < 0.021$, both cases; Figure 2), and

in the 24.1 cm dbh class Hi + B (4.4%) and HiD (4.1%) had significantly higher levels of bark beetle-caused tree mortality than LoD (1.1%) (Figure 2). No significant treatment effect was observed in the 44.5 cm dbh class ($P = 0.728$). A significantly higher percentage of bark beetle-caused tree mortality occurred on HiD + B compared to LoD + B in the two largest dbh classes ($P < 0.041$, both cases) (Figure 2). In addition, significantly higher levels of bark beetle-caused tree mortality occurred on HiD + B (5.3%) than LoD + B (0.9%) in the >59.7 cm dbh class (Figure 2). Approximately 65% (4472 trees) of all bark beetle-caused tree mortality occurred on burned split plots, primarily HiD + B.

Western Pine Beetle

Among all plots, 1.2% of ponderosa pines (1189 trees) were killed by WPB, of which 61.5% (731 trees) occurred on HiD + B, with 21.7%, 13.4%, and 3.4% occurring on HiD, LoD + B, and LoD, respectively. Overall, a significantly higher percentage of WPB-caused tree mortality occurred on HiD + B (2.8%) than HiD (0.8%) and LoD (0.5%) ($P = 0.018$; Figure 3). No other significant differences were observed. In the two smallest dbh classes, a significantly higher percentage of WPB-caused tree mortality occurred on HiD + B than LoD ($P < 0.031$, both cases), and in the 34.3 cm dbh class, LoD + B (2.7%) had significantly higher levels of WPB-caused tree mortality than LoD (0.7%) (Figure 3). No significant treatment effect was observed in the 44.5 cm dbh class ($P = 0.232$). A significantly higher percentage of WPB-caused tree mortality occurred on HiD + B (4.3%) than HiD (0.5%) and LoD + B (0%) in the 54.7 cm dbh ($P = 0.011$; Figure 3). In the largest dbh class, significantly higher levels of WPB-caused tree mortality occurred on HiD + B (5.2%) than any other treatment ($P = 0.020$; Figure 3). Approximately 75% (891 trees) of all WPB-caused tree mortality occurred on burned split

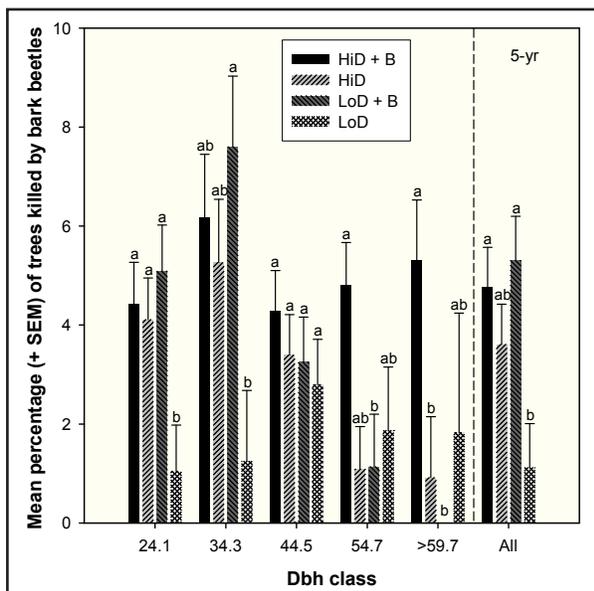


Figure 2. Mean percentage of trees killed by bark beetles (all bark beetle species combined) by diameter class (mid-point of 10 cm diameter classes shown except for largest diameter class), and for all trees by treatment (LoD, low structural diversity; HiD, high structural diversity; B, prescribed burn) five years after the application of prescribed fire, Blacks Mountain Experimental Forest, California, USA. Means (+ SE) followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$).

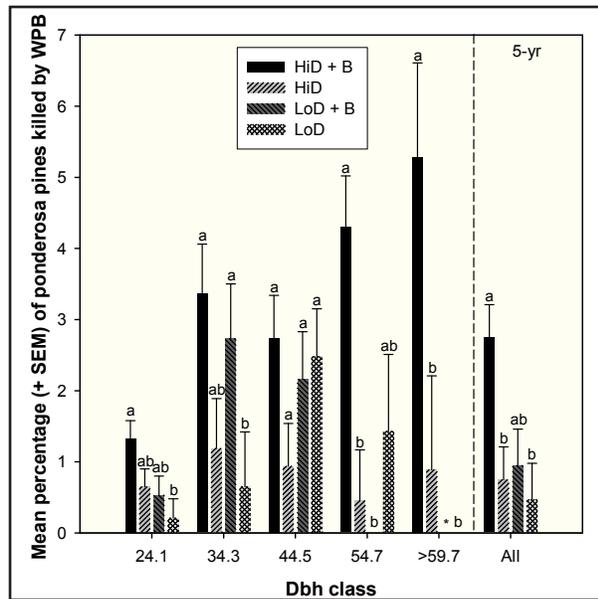


Figure 3. Mean percentage of ponderosa pines killed by western pine beetle (WPB) by diameter class (mid-point of 10 cm diameter classes shown except for largest diameter class), and for all trees by treatment (LoD, low structural diversity; HiD, high structural diversity; B, prescribed burn) five years after the application of prescribed fire, Blacks Mountain Experimental Forest, California, USA. Means (+ SE) followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$). Asterisk denotes no ponderosa pines existed in this dbh class within this treatment.

plots, primarily HiD + B. Most of this activity was concentrated in the largest dbh class ($P = 0.041$; Figure 4).

Mountain Pine Beetle

Among all plots, 1.4% of ponderosa pines (1415 trees) were killed by MPB, of which 40.7% (576 trees) occurred on HiD + B with 32.7%, 21.8%, and 4.8% occurring on HiD, LoD + B, and LoD, respectively. Overall, a significantly higher percentage of MPB-caused tree mortality occurred on HiD + B (2.1%) and LoD + B (1.8%) than LoD (0.5%) ($P = 0.046$; Figure 5). No other significant differences were observed (Figure 5). No significant treatment effects were observed in the 24.1 cm, 44.5 cm, and 54.7 cm dbh classes ($P > 0.101$). In the 34.3 cm dbh class, a significantly higher

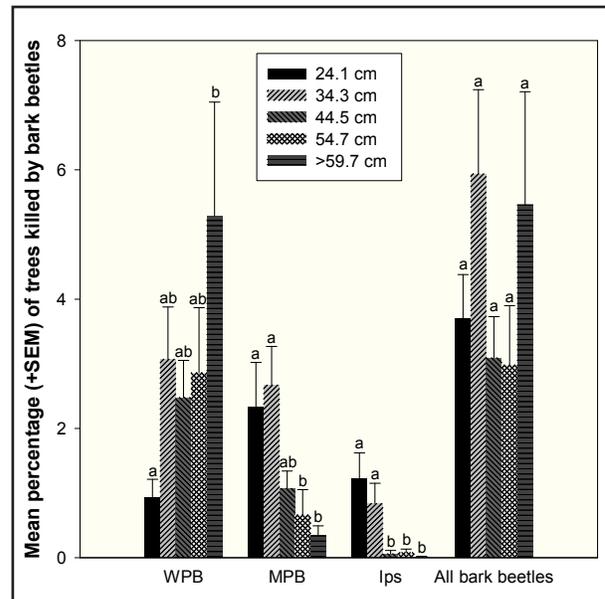


Figure 4. Colonization rates of available pines among diameter classes (mid-point of 10 cm diameter classes shown except for largest diameter class) on burned split plots for western pine beetle (WPB), mountain pine beetle (MPB), *Ips* spp. (*Ips*), and all bark beetle species combined, Blacks Mountain Experimental Forest, California, USA. Means (+ SE) followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$).

percentage of MPB-caused tree mortality occurred on HiD + B (2.8%) and LoD + B (2.7%) than LoD (0.6%) ($P = 0.018$; Figure 5). In the largest dbh class, a significantly higher percentage of MPB-caused tree mortality occurred on HiD + B (0.4%) than any other treatment ($P < 0.001$; Figure 5). Approximately 62% (884 trees) of all MPB-caused tree mortality occurred on burned split plots, primarily HiD + B. Most of this activity was concentrated in the smaller dbh classes ($P < 0.001$; Figure 4).

Jeffrey Pine Beetle

A total of 35 Jeffrey pines (0.2% of all Jeffrey pines) were killed by JPB and therefore statistical analyses were not conducted. Most of this mortality (85%) occurred on burned split plots.

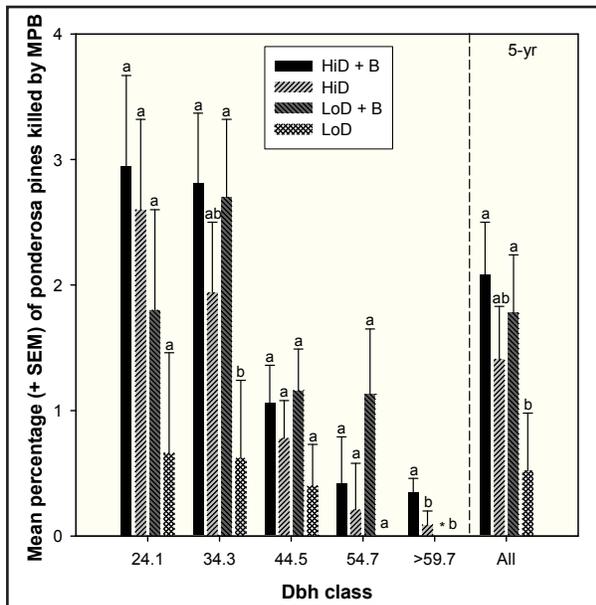


Figure 5. Mean percentage of ponderosa pines killed by mountain pine beetle (MPB) by diameter class (mid-point of 10 cm diameter classes shown except for largest diameter class), and for all trees by treatment (LoD, low structural diversity; HiD, high structural diversity; B, prescribed burn) five years after the application of prescribed fire, Blacks Mountain Experimental Forest, California, USA. Means (+ SE) followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$). Asterisk denotes no ponderosa pines existed in this dbh class within this treatment.

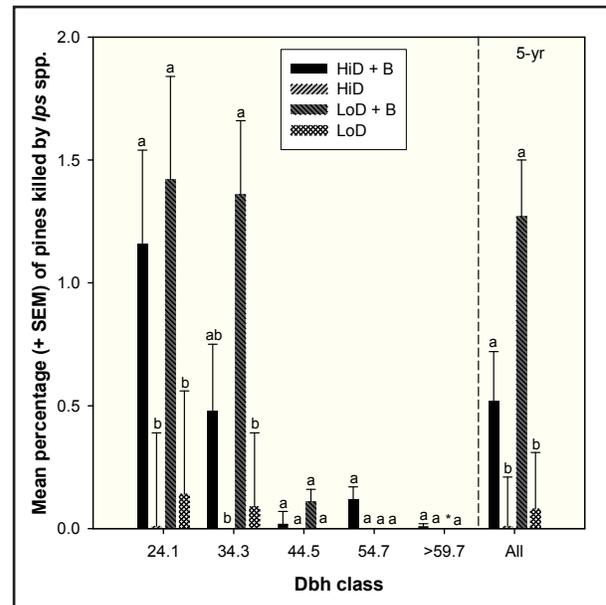


Figure 6. Mean percentage of pines killed by *Ips* spp. (*Ips*) by diameter class (mid-point of 10 cm diameter classes shown except for largest diameter class), and for all trees by treatment (LoD, low structural diversity; HiD, high structural diversity; B, prescribed burn) five years after the application of prescribed fire, Blacks Mountain Experimental Forest, California, USA. Means (+ SE) followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$). Asterisk denotes no pines existed in this dbh class within this treatment.

Ips spp.

Among all plots, 0.4% of all pines (471 trees) were killed by *Ips* spp., of which 65.4% (308 trees) occurred on LoD + B with 33.3% and 1.1% occurring on HiD + B and LoD, respectively. Only one tree was killed by *Ips* on HiD. Overall, a significantly higher percentage of *Ips*-caused tree mortality occurred on LoD + B (1.3%) and HiD + B (0.5%) than LoD (<0.1%) and HiD (<0.1%) ($P = 0.038$; Figure 6). A similar effect was observed in the smallest dbh class ($P = 0.015$; Figure 6). In the 34.3 cm dbh class, a significantly higher percentage of *Ips*-caused tree mortality occurred on LoD + B (1.4%) than LoD (0.9%) and HiD (0%) ($P = 0.002$; Figure 6). No significant treatment effects were observed in the

three largest dbh classes ($P > 0.247$, all cases). Approximately 99% (465 trees) of all *Ips*-caused tree mortality occurred on burned split plots, primarily LoD + B. Most of this activity was concentrated in the smaller dbh classes ($P < 0.001$; Figure 4).

Fir Engraver

A total of 3767 white firs (6.8% of all white firs) were killed by FE, of which 36.4% (1372 trees), 35.5%, 22.1%, and 6.0% occurred on HiD + B, HiD, LoD + B, and LoD, respectively. A significantly higher percentage of FE-caused tree mortality occurred on LoD + B (10.1%) than LoD (1.6%) ($P = 0.005$; Figure 7). No other significant differences were observed among treatments. In the small-

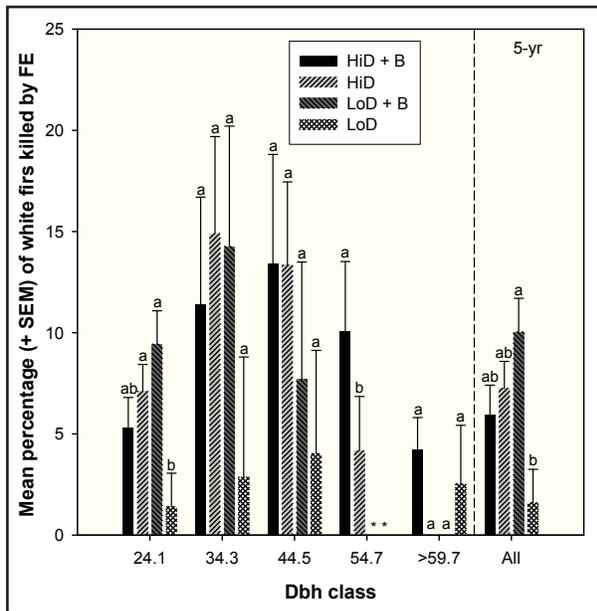


Figure 7. Mean percentage of white firs killed by fir engraver (FE) by diameter class (mid-point of 10 cm diameter classes shown except for largest diameter class), and for all trees by treatment (LoD, low structural diversity; HiD, high structural diversity; B, prescribed burn) five years after the application of prescribed fire, Blacks Mountain Experimental Forest, California, USA. Means (+ SE) followed by the same letter within groups are not significantly different (Tukey's HSD; $P > 0.05$). Asterisks denote no firs existed in this dbh class within these treatments.

est dbh class, a significantly higher percentage of FE-caused tree mortality occurred on LoD + B (9.4%) and HiD (7.1%) than LoD (1.4%) ($P = 0.008$; Figure 7). No significant treatment effects were observed in the 34.3 cm, 44.5 cm, and largest dbh classes (Figure 7). A significantly higher percentage of FE-caused tree mortality occurred on HiD + B (10%) than HiD (4.2%) in the 54.7 cm dbh class ($P = 0.002$; Figure 7). Approximately 58.5% (2203 trees) of all FE-caused tree mortality occurred on burned split plots, primarily Hi + D.

DISCUSSION

One of the primary objectives at BMEF was to create stand conditions that serve as a model of resiliency to wildland fire and insects

for interior ponderosa pine forests. The effectiveness of fuel reduction treatments to increase the resiliency of interior ponderosa pine forests to fire is well established (e.g., Agee and Skinner 2005, Ritchie *et al.* 2007), but may have unintended effects. For example, a common concern is that fire-injured trees may serve as breeding substrates for bark beetles that then attack adjacent trees or adjacent untreated areas at elevated levels. However, this has not been well documented in the scientific literature (Parker *et al.* 2006), perhaps due to the limited spatial and temporal scales of many studies. To that end, large numbers of severely stressed trees could provide abundant host material and once this resource has been exhausted (i.e., within one to two years following prescribed burns), bark beetles may attack and kill trees that might otherwise have survived. Breece *et al.* (2008) reported that prescribed burns increased bark beetle attacks on ponderosa pines over a three year period. Eighty percent of all bark beetle-attacked trees were colonized during the first year following the application of prescribed fire. During the second and third years, 8% and 12% were colonized, respectively (Breece *et al.* 2008). Fettig *et al.* (2010a) reported that the amount of bark beetle-caused tree mortality was evenly distributed two and four years after the application of thinning and burning treatments in the southern Cascades, USA. In the central Sierra Nevada, USA, it was reported that 38%, 42%, and 20% of bark beetle-caused tree mortality occurred during the first, second, and third years following prescribed fire, respectively (Fettig *et al.* 2010b). The authors commented that all of the delayed mortality attributed to bark beetle attack may not have been captured during the three-year period. We found that 37% and 63% of bark beetle-caused tree mortality occurred during our initial (one to two years after prescribed fire) and second surveys (three to five years), respectively, an effect similar (when adjusted for temporal scale) to that observed in a mixed conifer forest in Cali-

fornia (Fettig *et al.* 2010a). Unexpectedly, a large percentage of the total bark beetle-caused tree mortality that was recorded on HiD and LoD (84% and 88%, respectively) occurred three to five years after the application of prescribed fire to adjacent split plots. However, an unexpectedly low percentage of the total bark beetle-caused tree mortality recorded on LoD + B (38%) occurred three to five years after the application of prescribed fire. The effect of the Cone Fire on levels of bark beetle-caused tree mortality detected during our surveys conducted in 2004 and 2005 (i.e., 2 yr to 3 yr after the event; Table 1) cannot be determined. While fire-injured trees may serve as breeding substrates for bark beetles that then may attack trees in adjacent areas at elevated levels in subsequent years (Parker *et al.* 2006), much of the area affected by the Cone Fire was a stand replacing event. Furthermore, of the nine plots that were not directly affected by the Cone Fire, all except one (plot 45) are >1 km from affected areas and several are separated by a large meadow (Oliver 2000). We therefore feel that the Cone Fire likely had little effect on levels of bark beetle-caused tree mortality observed on our plots.

Levels of bark beetle-caused tree mortality increased substantially on unburned split plots compared to burned split plots following our initial survey. For example, in the HiD structure, we observed a 420% increase in the number of trees killed by bark beetles (333 versus 1731) between surveys on unburned split plots compared to a 50% increase (1139 versus 1718) on burned split plots. Similarly, in the LoD structure, we observed a >600% increase (41 versus 301) on unburned split plots compared to a 38% decrease (998 versus 616) on burned split plots. Trends were similar for all individual bark beetle species (i.e., WPB, MPB, and FE) except *Ips* spp. where 96% of all *Ips*-caused tree mortality was detected during our initial survey (Fettig *et al.* 2008). *Ips* spp. generally colonize slash, saplings, and weakened trees. 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 (Furniss and Carolin 1977). While concerns regarding *Ips*-population increases in logging slash and subsequent colonization of trees are important, prescriptions at BMEF included removal and utilization of slash following thinning. Accordingly, little or no slash was left within experimental plots to serve as breeding substrates for *Ips* beetles (Kegley *et al.* 1997, DeGomez *et al.* 2008). The response of *Ips* spp. to fuel reduction treatments at BMEF appears relatively short-lived and limited to fire-injured trees in the two smallest dbh classes (94% of all cases) (Fettig *et al.* 2008). However, the apparent shift in WPB, MPB, and FE activity from burned to unburned split plots three to five years after the application of prescribed fire is concerning, and warrants further monitoring of these plots. The effect is likely due to unburned areas not benefiting from the positive effects of prescribed fire (e.g., on growing space three to five years after treatment) that affect tree vigor and thus susceptibility to bark beetle attack (Fettig *et al.* 2007). Unburned areas (split plots) were adjacent to burned areas (split plots) that likely served as an important source of beetles once the abundance of fire-injured trees that were highly susceptible to bark beetle attack declined. Interestingly, Fettig *et al.* (2006) observed a similar effect (albeit on a much smaller spatial scale) in another study examining the effects of chipping of unmerchantable trees on bark beetle activity in ponderosa pine stands. In that study, chipping following thinning increased plot risk to bark beetle attack in the short-term by the production of large amounts of attractive monoterpenes. In the longer term, it decreased hazard by increasing the amount of growing space allocated to each residual tree. Surveys along the perimeter of chipped plots revealed large numbers of recently attacked trees in untreated areas that did not benefit from the positive ef-

fects of thinning, but suffered a similar level of risk associated with high levels of monoterpenes beneath the forest canopy.

Concerns about maintaining large-diameter pines, particularly in reference to delayed mortality attributed to bark beetle attack on HiD + B, were expressed among the interdisciplinary team. Larger trees are more fire-resistant (Peterson and Ryan 1986, Harrington 1993, Thies *et al.* 2005). Furthermore, tree species with thicker bark (e.g., ponderosa pine) are less likely to suffer fire-induced damage than thinner barked species (e.g., white fir) (Ryan and Reinhardt 1988, Ryan and Frandsen 1991). In the central Sierra Nevada, Regelbrugge and Conard (1993) reported decreased probability of post-fire mortality in ponderosa pine with increasing tree diameter and height. We observed no significant differences in the proportion of pines killed by bark beetles (all bark beetle species combined) among dbh classes following prescribed fire, but for WPB, MPB, and *Ips* spp. individually, an effect was observed (Figure 4). For MPB and *Ips* spp., mortality was aggregated in the smallest dbh classes, which agrees with their host preference for smaller diameter trees in interior ponderosa pine forests (Furniss and Carolin 1977). However, for WPB, significantly higher levels of tree mortality (5.3%) were observed for the largest dbh class, which differs from data from our initial survey (Fettig *et al.* 2008). The MPB frequently colonizes smaller diameter ponderosa pines in California, while WPB attacks are concentrated in the larger diameter classes (Miller and Keen 1960), which likely explains the different effects observed for these species. During our initial survey, 71 large dbh (>59.7 cm) ponderosa pines were killed by WPB on HiD + B and 9 on HiD. At the end of five years, 220 large dbh ponderosa pines had been killed by WPB on HiD + B and 53 on HiD. If this level continues, it will likely interfere with management objectives at BMEF that are aimed at maintaining large trees for fire resiliency and late-seral forest

conditions. Only one tree was killed by WPB on LoD plots in the two largest dbh classes, which is surprising given the beetle's preference for larger diameter trees (50.8 cm dbh to 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 dbh classes on LoD plots, respectively.

We caution the reader that bark beetle responses to silvicultural treatments, specifically prescribed burns, are heavily influenced by location as this dictates the bark beetle assemblages that are present (e.g., WPB does not occur throughout the entire range of ponderosa pine) and associated population levels during and after fire. In brief, interior ponderosa pine forests are recognized for the diversity of tree-killing bark beetle species inhabiting them, most notably WPB, MPB, JPB, PE, and FE. In Fettig *et al.* (2008), we emphasized that results pertained 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" following an earlier period of elevated activity. In 2001, activity of these species, with exception of JPB, began to slightly increase in portions of northeastern California (Fettig *et al.* 2008) and remained at somewhat elevated levels by the time our surveys were completed in 2005 (Forest Service 2010). 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). Much of northern California emerged from four years of drought with above normal precipitation in 2005. To that end, drought may have been an important factor influencing bark beetle activity during our second surveys, particularly for FE, which readily responds to drought stress in white fir (Berryman and Ferrell 1988). Interestingly, we ob-

served a 123% increase in FE-caused tree mortality three to five years following the application of prescribed fire (i.e., the period of time generally coinciding with drought) compared to a 32% increase in bark beetle-caused tree mortality in the pine component during the same period of time. Accordingly, we feel that the responses documented here occurred during bark beetle population pressures commonly observed in these forests. However, a more significant test of the resiliency of these treatments and resulting structures will occur if bark beetle populations build in the region.

Slightly more than half (6877 trees) of tree deaths were attributed to delayed mortality resulting from bark beetle attack. The relatively low amount (4.0%) of bark beetle-caused tree mortality is not surprising given the residual stand densities achieved in this study for both LoD and HiD (Oliver 2000, Zhang *et al.* 2008), and the strong relationship between stand density and tree and stand susceptibility to bark beetle attack. To that end, we observed no difference in the percentage of bark beetle-caused tree mortality between LoD and HiD except in the smallest dbh class (Figure 2), suggesting that the resiliency of these two structures to bark beetle infestations were similar over the five-year period. In Fettig *et al.* (2008), we concluded that near-term (two years following the application of prescribed fire) levels of bark beetle-caused tree mortality (1.5%) would not interfere with management objectives, particularly considering that almost half was represented by FE infesting white fir and treatments were designed to promote ponderosa and Jeffrey pines over white fir. At that time, we issued a caveat that the effects of RTB attacks and prescribed fire on individual tree health and on subsequent levels of tree mortality may not be realized for some time. Eighty-one percent of all RTB-attacked trees over the five-year period were recorded during our initial survey, and we saw no evidence of trees that were attacked by RTB dying in the absence of

attacks by other bark beetle species or confounding factors (e.g., mechanical damage).

Fettig *et al.* (2008) reported that wood borer attacks directly contributed to tree mortality in numerous fire-injured trees at BMEF during the second year after the application of prescribed fire, and that in the absence of such attacks tree mortality would likely not have occurred. However, this effect was not observed during our second survey or in a similar study conducted in the southern Cascades (Fettig *et al.* 2010a). While a body of literature is building concerning evidence of wood borers directly contributing to tree mortality in fire-injured trees (Parker *et al.* 2006), the effect, when it occurs, seems to be short-lived, occurring immediately after disturbance.

Two years after the application of prescribed fire at BMEF, we (Fettig *et al.* 2008) concluded that concerns regarding delayed mortality of large diameter ponderosa and Jeffrey pines at BMEF were unfounded. However, we issued a caveat that this relationship could change in the future, particularly if significant root damage had occurred as a result of the application of prescribed fire. The increased rates of mortality attributed to WPB attacks in the large tree component following prescribed fire (Figures 3 and 4) is concerning and may be occurring as a result of greater basal duff accumulations resulting in increased fire intensity and fine root injury, and thus reduced tree vigor. Swezy and Agee (1991) reported lethal heat loads occurred in >75% of samples at the soil interface and at 5 cm soil depth following the application of prescribed fire in old-growth ponderosa pines at Crater Lake National Park, USA. Similar effects have been observed in other pine systems (Sullivan *et al.* 2003). We intend to continue monitoring these plots in the future to determine the longer-term effects of these treatments and the resulting stand structures on the amount of bark beetle-caused tree mortality, particularly in the large tree component.

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