

Effects of Fire and Fire Surrogate Treatments on Bark Beetle-Caused Tree Mortality in the Southern Cascades, California

Christopher Fettig, Robert Borys, and Christopher Dabney

Abstract: We examined bark beetle responses to fire and fire surrogate treatments 2 and 4 years after the application of prescribed fire in a mixed-conifer forest in northern California. Treatments included an untreated control (C), thinning from below (T), and applications of prescribed fire (B) and T + B replicated three times in 10-ha experimental units. A total of 1,822 pine and fir trees (5.1% of all trees) were killed by bark beetles. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) was found infesting ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), sugar pine (*Pinus lambertiana* Dougl.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.); western pine beetle (*Dendroctonus brevicomis* LeConte) was found infesting ponderosa pine; and fir engraver (*Scolytus ventralis* LeConte) was found infesting white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.). Significantly higher rates of bark beetle-caused tree mortality occurred on B (9.2%) than on C (3.2%), T (<1%), or T + B (3.3%) cumulatively during the 4-year period. A total of 723 pines (4.4% of all pines) were killed by bark beetles, primarily mountain pine beetle. Attacks resulted in significantly more pine mortality on B (5%) than on C, T, or T + B (all <1%) 2 years after the application of prescribed fire. No significant treatment effects were found during the second sample period or cumulatively during the 4-year period. A total of 1,098 white fir trees (5.8% of all white fir) were killed by the fir engraver. Attacks resulted in significantly higher rates of fir mortality on T + B than on T during both sample periods but not cumulatively during the 4-year period. Overall, bark beetle-caused tree mortality was concentrated in the smaller diameter classes. The implications of these and other results to forest management are discussed. FOR. SCI. 56(1):60–73.

Keywords: prescribed fire, thinning, *Dendroctonus ponderosae*, *Dendroctonus brevicomis*, *Scolytus ventralis*

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 tree mortality agents (Furniss and Carolin 1977). To reproduce, bark beetles must successfully locate suitable and susceptible hosts using a variety of behavioral modalities. In the case of living hosts, colonization requires overcoming tree defenses (Franceschi et al. 2005) by recruitment of a critical minimum number of beetles to mass attack individual trees. This threshold varies with changes in host tree vigor. Depending on the bark beetle species and numerous other factors (Fettig et al. 2007), the extent of tree mortality may be limited to small spatial scales (e.g., individual trees or small groups of trees) that often go unnoticed or affect large areas (e.g., >9 million ha) such as recently observed in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests of British Columbia, Canada (Westfall and Ebata 2008).

Forest management influences the amount and distribution of bark beetle-caused tree mortality at various spatial and temporal scales. For example, silvicultural treatments

may affect the health, vigor, and defenses of residual trees (Vité and Wood 1961, Smith 1975, McDowell et al. 2007), the size, distribution, and abundance of preferred hosts (Fettig et al. 2007), and the physical environment within forest stands, which influences microclimate (Bartos and Amman 1989). Microclimate affects beetle fecundity and fitness, phenology, and voltinism as well as that of predators, parasites, and competitors (Amman 1989, Bartos and Amman 1989) or may cause turbulences that disrupt pheromone plumes used for recruiting conspecifics during the initial phases of host tree colonization (Thistle et al. 2004). 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 subcortical insects and root pathogens. Furthermore, tree volatiles released during harvest operations include monoterpenes, which influence the physiology and behavior of bark beetles (Seybold et al. 2006) and may increase rates of bark beetle attack (Fettig et al. 2006) and associated levels of tree mortality after certain treatments (DeGomez et al. 2008).

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In recent years, unusually large and catastrophic wildfires have heightened public concern. Such events emphasize the need for well-designed silvicultural treatments to reduce their extent and severity. Mechanical fuel treatments (e.g., thinning from below) and the application of prescribed fire are commonly used to reduce the accumulation of hazardous fuels, enhance wildlife habitat, and restore fire-adapted forest ecosystems. However, sublethal heating of critical plant tissue during prescribed burns can stress trees, which then may become more susceptible to bark beetle attack (Parker et al. 2006, Breece et al. 2008). In the central Sierra Nevada of California, Schwilk et al. (2006) found the probability of bark beetle attack (several species) on pines did not differ between early and late season burns, whereas the probability of attack on firs (*Abies* spp.) was greater after early season burns. Fettig et al. (2008) reported the application of prescribed fire resulted in significant increases in bark beetle-caused tree mortality (all species) and for western pine beetle (WPB) (*Dendroctonus brevicomis* LeConte), mountain pine beetle (MPB) (*D. ponderosae* Hopkins), engraver beetles (*Ips* spp.), and fir engraver (FE) (*Scolytus ventralis* LeConte) individually in interior ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*) forests of northern California. The propensity for bark beetles to attack fire-injured trees in the western United States has led to questions regarding how the amount and distribution of bark beetle-caused tree mortality will be affected by the large-scale restoration of fire-adapted forest ecosystems by prescribed fire (Parker et al. 2006).

Forest health professionals have generally recognized that stand susceptibility to bark beetle attack can be manipulated by addressing factors related to tree density (Fettig et al. 2007). Sartwell (1971) presented data on radial growth and its relationship to MPB attack and suggested that slow growth was indicative of nearly all trees killed by MPB in the Pacific Northwest. Sartwell concluded that thinning to reduce tree competition and increase individual tree growth was critical to reducing stand susceptibility to MPB attack. Feeney et al. (1998) assessed the effects of thinning from below (alone and in combination with prescribed burning) on tree growth in northern Arizona and suggested that restoration treatments improved tree vigor and growth and decreased the likelihood of bark beetle attacks on individual trees. Several recent studies support these conclusions (e.g., Kolb et al. 1998, Stone et al. 1999, Wallin et al. 2004, 2008, Sala et al. 2005, Skov et al. 2005, Zausen et al. 2005). Alternatively, Sánchez-Martínez and Wagner (2002) studied the abundance of bark beetle-attacked trees in managed and unmanaged stands in northern Arizona. These authors detected no significant difference in the amount of bark beetle-caused tree mortality among treatments, although bark beetle populations were endemic during the study period. Fettig et al. (2008) reported that there was no significant difference in the mean percentage of trees killed by bark beetles several years after the creation of mid-seral (low structural diversity) and late-seral (high structural diversity) stand conditions in interior ponderosa pine. Low structural diversity was created by removing larger overstory trees in addition to small understory trees, leaving only

trees of intermediate size, whereas high structural diversity was attained by thinning smaller and retaining larger trees.

Our work is part of the Fire and Fire Surrogate (FFS) Study (2008), a national network of 12 long-term study sites established to evaluate the ecological and economic consequences of treatments intended to reduce fuels and restore forest ecosystems. The objective of this particular study was to determine the response of bark beetles to fuel reduction treatments 2 and 4 years after the application of prescribed fire in a mixed-conifer forest at the Southern Cascades FFS site in northern California.

Materials and Methods

Study Site and Treatments

The Southern Cascades site, located on the Goosenest Adaptive Management Area (GAMA) (41°30'N, 121°52'W; 1,500–1,780 m elevation) of the Goosenest Ranger District, Klamath National Forest, California, was selected as one of the original sites in the FFS national network (McIver and Weatherspoon 2009). Adaptive management areas were established to provide forest managers with areas in which to test and evaluate different forest management activities. Average annual precipitation at GAMA is ~75 cm coming mostly as snow in winter. Estimated presettlement fire return intervals were 5–35 years, depending on forest type and spatial scale (Skinner and Chang 1996). GAMA was historically dominated by ponderosa pine; however past effects of selective logging of large-diameter (>76.2 cm dbh, diameter at 1.37 m in height) ponderosa pine in the early to mid-20th century and highly effective fire suppression, among other factors, have resulted in substantial changes in forest structure and composition (Ritchie 2005). Today, GAMA is dominated by white fir (*Abies concolor* [Gord. & Glend.] Hildebr.) and to a lesser extent by ponderosa pine, sugar pine (*Pinus lambertiana* Dougl.), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), and lodgepole pine. Western juniper (*Juniperus occidentalis* Hook.), red fir (*Abies magnifica* A. Murr.), and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) also occur, but are rare, representing <1% of all trees. Red fir occurs only at the highest elevations, whereas lodgepole pine is restricted to sites where cold air tends to pool (Ritchie 2005).

The core experimental design for the FFS study includes common treatments, similar replication and plot sizes, and common response variables for all research sites in the network (McIver and Weatherspoon 2009). At each site, implementation of treatments (exclusive of the untreated control) was guided by a desired future condition or target stand condition uniquely defined for each stand such that if a stand were affected by a head fire under 80th percentile weather conditions ≥80% of the basal area of overstory trees would survive. At the Southern Cascades site, these included: (1) untreated control—no manipulation (C), (2) burn—prescribed burning in the fall (B), (3) thin—thinning from below and selection harvest with leave trees including all stems >76.2 cm dbh regardless of tree species, all sugar pine and incense cedar, and all codominant and dominant ponderosa pine (T), and (4) T + B—thinning from below

and selection harvest followed by prescribed fire in the fall. Each treatment was randomly assigned to three experimental units ($n = 12$) 10-ha in size exclusive of buffers (Table 1). More complete descriptions of treatments and pretreatment and posttreatment stand conditions are available elsewhere (McIver 2001, Ritchie 2005).

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 tree mortality. Although incense cedar, western juniper, and Douglas-fir (one tree recorded) are minor components of the Southern Cascades site, these species generally are not attacked and killed by bark beetles in northern California and were ignored in surveys and subsequent analyses. Cruises were conducted during the second and fourth year (field season) after the application of prescribed fire (Table 1). In northern California, 2 years is sufficient to allow distinction between crown scorch resulting from prescribed burns and crown fade associated with tree mortality attributable to bark beetle attack or other factors (Fettig et al. 2008). During the second sampling period, only mortality that occurred in years 3 and 4 after the application of prescribed fire was recorded. All recently killed pine and fir trees >19 cm dbh were identified and tallied and the causal agent of mortality was recorded. Tree species, dbh, crown color, colonizing bark beetle species, the presence of wood borers (Coleoptera: Cerambycidae, Buprestidae), and ranking of burn severity based on external bole characteristics (Fettig et al. 2002, 2008) were recorded. A section of bark approximately 625 cm² was removed with a hatchet at 2 m in height on at least two aspects to determine whether 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. In addition, the 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 was recorded (Furniss and Carolin 1977). On occasion, other bark beetle genera (e.g., *Hylastes*, *Hylurgops*, and *Pseudohylesinus*) were found colonizing trees that had been killed by prescribed burns or other bark beetles. In general, these groups are not considered primary tree killers (i.e., a generic term used to describe bark beetle species [e.g., MPB and WPB] that are capable of killing apparently healthy trees and causing widespread tree mortality) and were ignored.

The precise role of each bark beetle species in causing tree mortality is uncertain as attacks by several species often occur within the same tree. Accordingly, in reference to MPB, WPB, 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 (16 and 29 trees for sample periods 1 and 2, respectively), we found MPB and WPB infesting the same ponderosa pine. In these situations, we attributed tree mortality to MPB when trees were <31.8 cm dbh and WPB when ≥ 31.8 cm dbh. For pines, mortality was only attributed to *Ips* spp. when evidence of MPB and WPB colonization were absent and another causal agent of mortality could not be identified. Mortality was only attributed to MPB, WPB, FE, and *Ips* spp. when burn severity rankings on individual trees were ≤ 3 (Fettig et al. 2002, 2008). A ranking of 4 indicates that the tree was directly killed by prescribed fire, regardless of any evidence of bark beetle attack, as indicated by external measures of fire severity (i.e., charring of bark plates and fissures with substantial bark consumption; Fettig et al. 2002). Therefore, a distinction is made for those trees immediately killed by prescribed fire and those predisposed by fire to bark beetle attack (Ganz et al. 2003). Mortality was not attributed to RTB or any other bark beetle except MPB, WPB, FE, and *Ips* spp.

For purpose of this study, primary variables of interest were the mean percentage of trees killed by all bark beetle

Table 1. Post-treatment stand conditions and evaluation dates, Southern Cascades site, Klamath National Forest, California

Treatment ¹	Trees (/ha)	BA (m ² /ha)	QMD (cm)	SDI	Harvest date	Burn date	Census Date ²	
							First	Second
						(mo/yr).....		
Control	539.9	43.0	31.9	307.0	—	—	7/2003	7/2005
Control	623.9	40.1	28.6	301.8	—	—	7/2003	7/2005
Control	1,010.1	49.9	25.1	401.1	—	—	7/2003	7/2005
Burn	652.1	31.2	24.7	252.9	—	10/2002	6/2004	8/2006
Burn	804.1	48.8	27.8	372.6	—	10/2002	8/2004	8/2006
Burn	996.1	58.7	27.4	451.7	—	10/2002	8/2004	8/2006
Thin	195.0	25.2	40.6	159.4	9/1999	—	7/2003	8/2005
Thin	227.1	38.8	46.7	228.8	11/1998	—	7/2003	8/2005
Thin	194.0	27.5	42.5	169.7	7/1999	—	6/2003	8/2005
Thin + burn	179.9	25.5	42.4	157.3	12/1998	10/2001	7/2003	6/2005
Thin + burn	175.9	20.8	38.8	134.6	10/1999	10/2001	7/2003	6/2005
Thin + burn	123.6	18.5	43.6	112.6	8/1999	10/2001	7/2003	7/2005

BA, basal area; QMD, quadratic mean diameter; SDI, stand density index

¹ Control, no manipulation; burn, prescribed burn in fall; thin, thinned from below; thin + burn, thinned from below followed by prescribed burn in fall.

² Experimental units were cruised the second and fourth field season after implementation of prescribed burn treatments. 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.

species across all tree species, individual bark beetle and tree species, and individual bark beetle by tree species and diameter class (19–29.2, 29.3–39.3, 39.4–49.5, and >49.5 cm dbh). The experimental design was completely randomized with four treatments and three replicates per treatment ($df = 3, 8$). Tests of normality were performed and appropriate transformations were used when data deviated significantly from a normal distribution (arcsine square root [percentages]; Sokal and Rohlf 1995). We performed an analysis of variance on each response variable at $\alpha = 0.05$ (SigmaStat version 2.0; SPSS, Inc., Chicago, IL). If a significant treatment effect was detected, Tukey's multiple comparison test (Tukey's honestly significant difference) was used for separation of treatment means requiring more than one comparison. Relationships between measures of stand density and bark beetle-caused tree mortality were analyzed using Pearson's correlation coefficient (r) (SigmaStat version 2.0) and regression analyses for correlations that were statistically significant. To maintain conclusions of ecological significance, we limited analyses to bark beetle-host complexes (e.g., MPB in ponderosa pine) for which >25 trees were colonized among all experimental units during each sample period.

Results and Discussion

During this study, tree mortality was attributed to MPB in ponderosa (519 trees), sugar (27 trees), and lodgepole (9 trees) pines; WPB in ponderosa pine (159 trees); and FE in white (1,098 trees) and red (1 tree) fir. In rare cases, we attributed tree mortality to pine engraver (PE) (*Ips pini* [Say]) and emarginate ips (*I. emarginatus* [LeConte]) in ponderosa pine (6 and 2 trees, respectively), and *I. latidens* (LeConte) in lodgepole pine (1 tree). Although the California fivespined ips (*I. paraconfusus* Lanier) is indigenous to this area (Furniss and Carolin 1977) and substantial numbers have been collected in pheromone-baited traps in nearby areas (~22 km southwest) (Fettig et al. 2004b), we did not observe any trees that were attacked by *I. paraconfusus*.

Bark Beetle-Caused Tree Mortality—Pine and Fir

A total of 1,822 pine and fir trees (5.1% of all trees) were killed by bark beetles (all species combined) among all experimental units at the end of 4 years. During the initial sample period, we observed a significant treatment effect in the amount of bark beetle-caused tree mortality for all dbh classes combined ($F_{3,8} = 14.8$, $P = 0.001$) and within individual dbh classes ($P < 0.02$, all cases) (Fig. 1A). Significantly higher levels of bark beetle-caused tree mortality occurred on B than on any other treatment, except within the smallest dbh class for which B was only significantly different from T (Fig. 1A). Mean levels of bark beetle-caused tree mortality ranged from <1% (several treatments) to 8.4% (B, smallest dbh class). Little bark beetle-caused tree mortality was observed on T (Fig. 1A).

During the second sample period, no significant treatment effects were observed ($P > 0.20$, all cases). We

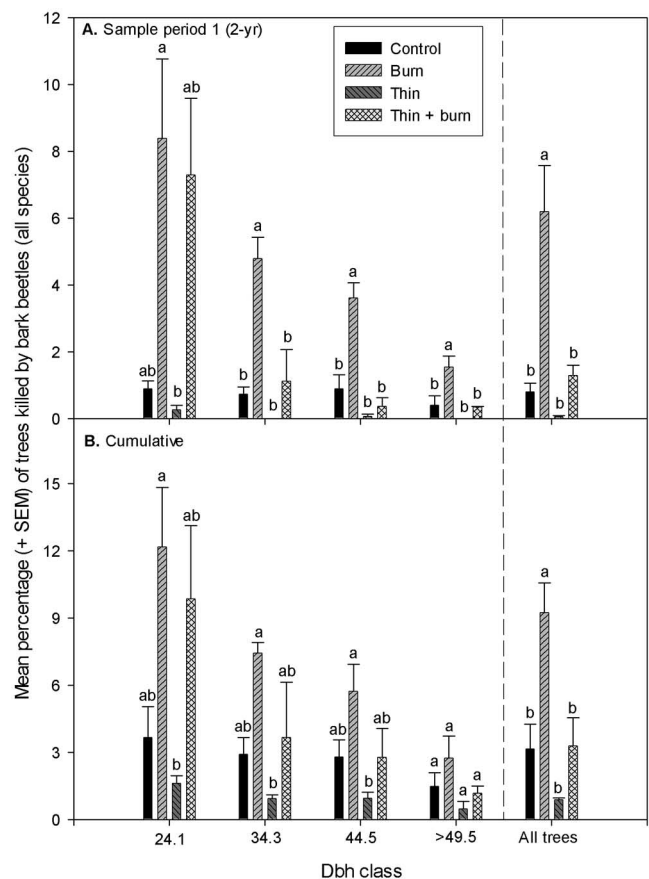


Figure 1. Mean percentage of trees killed by bark beetles (all bark beetle species combined) by diameter class (midpoint of 10-cm diameter classes shown except for largest diameter class) for evaluations completed 2 (A, sample period 1) and 4 years (B, cumulative [sample periods 1 + 2]) after prescribed burns were implemented, Southern Cascades site, Klamath National Forest, California. Treatments included: (1) untreated control—no manipulation, (2) burn—prescribed burned in fall, (3) thin—thinned from below, and (4) thin + burn. Means (+ SEM) followed by the same letter within groups are not significantly different ($P > 0.05$).

observed a significant treatment effect in the amount of bark beetle-caused tree mortality for all dbh classes combined ($F_{3,8} = 11.2$, $P = 0.003$) and within individual dbh classes ($P < 0.05$, all cases), except the largest dbh class (Fig. 1B), during the cumulative 4-year period (sample period 1 + 2). Higher levels of bark beetle-caused tree mortality occurred on B than on T (three smallest dbh classes) and C, T, and T+B (all dbh classes combined), respectively (Fig. 1B). Approximately 74.9% (1,364 trees) of all bark beetle-caused tree mortality occurred on experimental units that were prescribed burned (B and T+B).

Fettig et al. (2008) reported that 1.5% of trees were colonized by bark beetles (all species) in a large study (1,292 ha) in which experiment units were thinned and then half of which were prescribed burned. In their study, 85.6% of all bark beetle-caused tree mortality occurred on burned split plots. In an adjacent Research Natural Area, the percentage of trees killed by bark beetles was 3.3% 2 years after the application of prescribed fire and in the absence of prior mechanical thinning. In Arizona and New Mexico, prescribed burns increased the proportion of successful,

lethal attacks on ponderosa pine from 0.4 to 7.6% during the initial 3 years after treatments were implemented (Breece et al. 2008).

Bark Beetle-Caused Tree Mortality—Pine

At GAMA, stands formerly dominated by large-diameter (>76.2 cm dbh) ponderosa pine growing in relatively open conditions have been replaced by dense second-growth stands heavily represented by white fir (Ritchie 2005). Accordingly, fuel reduction treatments were also implemented with a restoration component that called for retaining all large trees, all sugar pines, and all codominant and dominant ponderosa pines (Ritchie 2005). Therefore, we were specifically interested in determining the effects of FFS treatments on the amount of bark beetle-caused tree mortality in the pine component, particularly within large trees, at Southern Cascades.

A total of 723 pines (4.4% of all pines) were killed by MPB, WPB, and *Ips* spp. among all experimental units. During the initial sample period, we observed a significant treatment effect in the amount of bark beetle-caused pine mortality for all dbh classes combined ($F_{3,8} = 50.4$, $P < 0.001$) and within individual dbh classes ($P < 0.05$, all cases). Significantly higher levels of bark beetle-caused tree mortality occurred on B than on any other treatment in the smallest and largest dbh classes and for all dbh classes combined (Fig. 2). For the 34.3 cm dbh class, significantly higher levels of bark beetle-caused tree mortality occurred on B than on C or T+B, whereas B was only significantly different from T within the 44.5 cm dbh class (Fig. 2). Mean levels of bark beetle-caused tree mortality ranged from <1% (several treatments) to 6.0% (B, two smallest dbh

classes). Only one tree was killed by bark beetles on T (Fig. 2).

No significant treatment effects were observed during the second sample period ($P > 0.24$, all cases) or cumulatively during the 4-year period ($P > 0.069$, all cases). Approximately 58.6% (424 trees) of all bark beetle-caused tree mortality occurred on experimental units that were prescribed burned (B and T+B). Oester et al. (2005) examined the effects of different thinning strategies on growth and yield of ponderosa pine in northeastern Oregon. The highest levels of bark beetle-caused tree mortality occurred in the control and were caused primarily by MPB and PE colonizing intermediate and suppressed trees. We observed no significant differences between C and T in our study.

MPB

The MPB occurs throughout British Columbia and Alberta, Canada, most of the western United States, and into northern Mexico and colonizes several pines, most notably lodgepole, ponderosa, sugar, whitebark (*Pinus albicaulis* Engelm.) and western white pine (*P. monticola* Dougl. ex D. Don) (Furniss and Carolin 1977). Most large-scale MPB infestations occur in mature lodgepole pine stands in a near-contiguous pattern and often across extensive areas (Westfall and Ebata 2008). The role of MPB in ponderosa pine stands in California is usually secondary to that of WPB (Miller and Keen 1960), particularly in larger diameter trees. In California, MPB infestations are typically confined to small-diameter (<31.8 cm dbh) ponderosa pines with single trees or small groups of trees being killed (Furniss and Carolin 1977).

A total of 519 ponderosa pines (3.3% of all ponderosa pine) were killed by MPB among all experimental units, and although sugar (27 trees) and lodgepole (9 trees) pines were also infested, their frequency was insufficient to permit statistical analyses (≤ 25 trees per sample period among all experimental units). During the initial sample period, we observed a significant treatment effect in the amount of MPB-caused tree mortality for all dbh classes combined ($F_{3,8} = 18.2$, $P < 0.001$) and for the two smallest dbh classes ($P < 0.022$, both cases). Significantly higher levels of MPB-caused tree mortality occurred on B than on any other treatment in the 24.1 cm dbh class and for all dbh classes combined (Fig. 3). For the 34.3 cm dbh class, B was only significantly different from C and T+B (Fig. 3). Mean levels of MPB-caused tree mortality ranged from 0% (several treatments) to 4.8% (B, smallest dbh class) during the first sample period.

No significant treatment effects were observed during the second sample period ($P > 0.24$, all cases) or cumulatively during the 4-year period ($P > 0.09$, all cases). Approximately 54.9% (285 trees) of all ponderosa pine mortality attributed to MPB occurred on B and T+B. Fettig et al. (2008) reported that the application of prescribed fire resulted in significant increases in MPB-caused tree mortality except within the two largest dbh classes (49.6–59.7 and >59.7 cm dbh), which agrees with our results (Fig. 3). In their study, approximately 83.3% of all MPB-caused tree

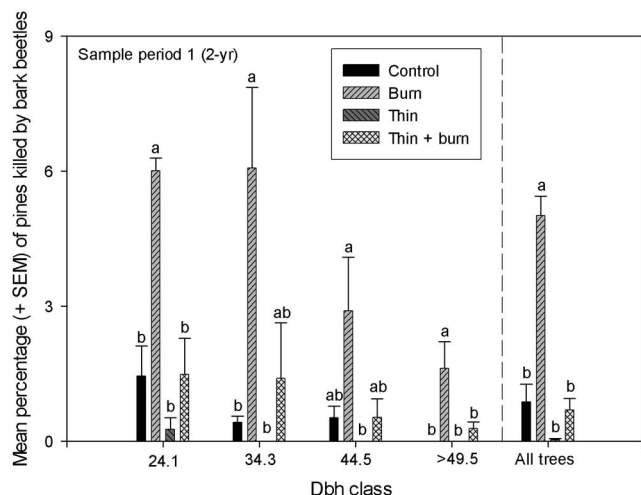


Figure 2. Mean percentage of pines killed by bark beetles by diameter class (midpoint of 10-cm diameter classes shown except for largest diameter class) for evaluations completed 2 years after prescribed burns were implemented, Southern Cascades site, Klamath National Forest, California. Treatments included: (1) untreated control—no manipulation, (2) burn—prescribed burned in fall, (3) thin—thinned from below, and (4) thin + burn. Means (+ SEM) followed by the same letter within groups are not significantly different ($P > 0.05$).

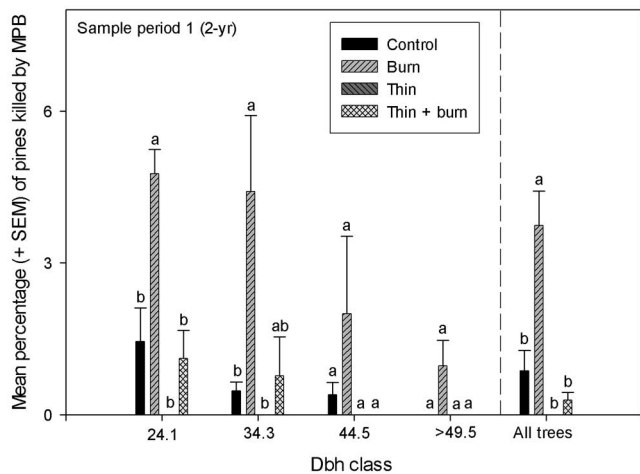


Figure 3. Mean percentage of pines killed by MPB (*D. ponderosae*) by diameter class (midpoint of 10-cm diameter classes shown except for largest diameter class) for evaluations completed 2 years after prescribed burns were implemented, Southern Cascades site, Klamath National Forest, California. Treatments included: (1) untreated control—no manipulation, (2) burn—prescribed burned in fall, (3) thin—thinned from below, and (4) thin + burn. Means (+ SEM) followed by the same letter within groups are not significantly different ($P > 0.05$).

mortality occurred on burned split plots. Alternatively, others have failed to demonstrate a positive response by MPB to fire-injured trees (Rasmussen et al. 1996, McHugh et al. 2003, Elkin and Reid 2004).

WPB

A total of 159 ponderosa pines (1.0% of all ponderosa pines) were colonized by WPB among all experimental units. The WPB is a major cause of ponderosa pine mortality in portions of the western United States (Miller and Keen 1960). Under certain conditions, the beetle can aggressively attack and kill apparently healthy trees of all ages and size classes. Recently, the amount of WPB-caused tree mortality reached unprecedented levels in the mountains of southern California where ~61,000 ha were infested (US Forest Service 2002). During the initial sample period, we observed a significant treatment effect in the amount of WPB-caused tree mortality for all dbh classes combined ($F_{3,8} = 16.8$, $P < 0.001$) and within the three smallest dbh classes ($P < 0.022$, all cases). Significantly higher levels of WPB-caused tree mortality occurred on B than on any other treatment for the 44.5 cm dbh class and for all dbh classes combined (Fig. 4A). In the two smallest dbh classes, B was only significantly different from C and T (Fig. 4A). Mean levels of WPB-caused tree mortality ranged from 0% (several treatments) to 1.3% (B, 34.3 cm dbh class) during this time. The lack of a significant treatment effect in the largest dbh class ($F_{3,7} = 2.2$, $P = 0.18$) is surprising, given the beetle's preference for larger diameter trees (50.8–81.3 cm dbh) (Person 1928), and may be an artifact of low attack rates, high variation and the loss of one replication in this size class (i.e., one experimental unit had no ponderosa pine >49.5 cm dbh).

No significant treatment effects were observed during

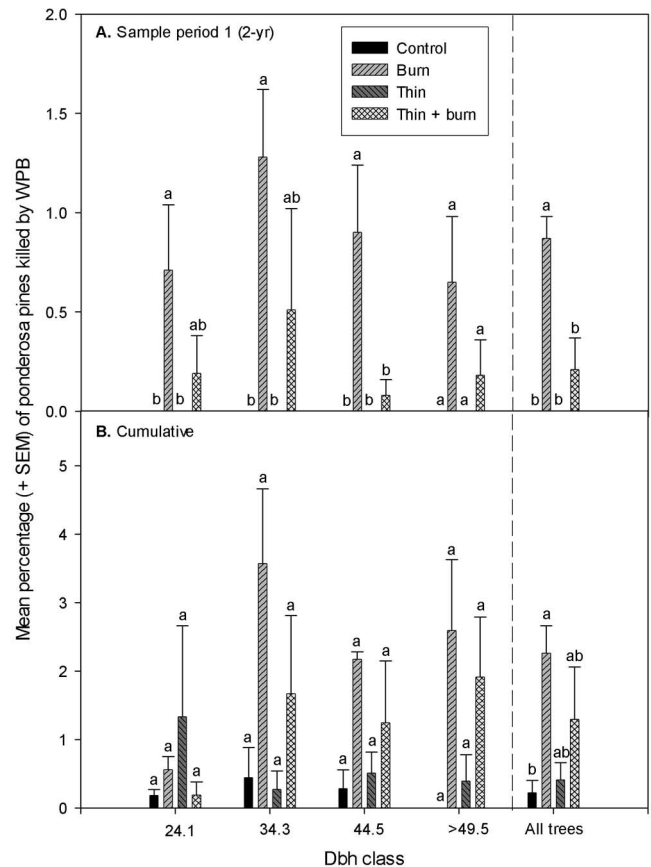


Figure 4. Mean percentage of ponderosa pines killed by WPB (*D. brevicornis*) by diameter class (midpoint of 10-cm diameter classes shown except for largest diameter class) for evaluations completed 2 (A, sample period 1) and 4 years (B, cumulative [sample periods 1 + 2]) after prescribed burns were implemented, Southern Cascades site, Klamath National Forest, California. Treatments included: (1) untreated control—no manipulation, (2) burn—prescribed burned in fall, (3) thin—thinned from below, and (4) thin + burn. Means (+ SEM) followed by the same letter within groups are not significantly different ($P > 0.05$).

the second sample period ($P > 0.13$, all cases) or cumulatively during the 4-year period ($P > 0.075$) except for all dbh classes combined ($F_{3,8} = 4.2$, $P = 0.048$) (Fig. 4B). Significantly higher levels of WPB-caused tree mortality occurred on B than on C (Fig. 4B). Mean levels of WPB-caused tree mortality ranged from <1% (C and T) to 2.3% (B). Approximately 81.8% (130 trees) of all WPB-caused tree mortality occurred on experimental units that were prescribed burned (B and T+B). McHugh et al. (2003) reported that WPB colonized only 3 of 222 trees after a prescribed fire on the Coconino National Forest in Arizona during endemic populations. Sánchez-Martínez and Wagner (2002) studied the relative abundance, based on trap catch, of bark beetles (several species) and bark beetle-attacked trees between managed and unmanaged stands in northern Arizona. Significantly more southern pine beetle (*Dendroctonus frontalis* Zimmerman) and WPB (combined) were collected in baited multiple-funnel traps in thinned and thinned and burned stands. However, these authors detected no significant difference in the amount of bark beetle-caused tree mortality during endemic population levels, but

others have established a link between fire injury and the increased susceptibility of ponderosa pine to WPB attack (e.g., Miller and Patterson 1927, Miller and Keen 1960, Fischer 1980). Fettig et al. (2008) reported that the application of prescribed fire resulted in a significant increase in WPB-caused tree mortality but not in the two largest diameter classes (49.6–59.7 and >59.7 cm dbh). In their study, 96.2% of all WPB-caused tree mortality occurred on burned split plots.

Ips spp.

Ips spp. generally colonize slash, saplings, and weakened trees or trees previously colonized by other bark beetle species. 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. In our study, few pines (nine trees) were killed by *Ips* spp. Although concerns regarding *Ips* population increase in logging slash and subsequent colonization of residual leave trees are important, harvest criteria (T and T+B) at Southern Cascades required that whole trees were skidded to a landing and then trucked to staging areas where de-limbing, bucking, and sorting of forest products occurred (Ritchie 2005). Accordingly, little or no slash was left within experimental units to serve as breeding substrates for *Ips* beetles (Kegley et al. 1997, DeGomez et al. 2008). However, the lack of *Ips* attacks in B (eight trees) is surprising, given results demonstrated in similar studies. For example, Ganz et al. (2003) studied effects of prescribed fire on susceptibility of ponderosa and Jeffrey (*Pinus jeffreyi* Grev. & Balf.) pines to bark beetle attack. Greater than 30% of pines were killed by PE the first year after prescribed burns. Fettig et al. (2008) reported that the application of prescribed fire resulted in a significant increase in the proportion of pines (>19 cm dbh) killed by *Ips* spp. with ~99% (491 trees) of all *Ips*-caused tree mortality occurring on burned split plots. Harvest criteria in their study also included removal and utilization (i.e., biomass or chips) of slash after thinning.

PE most frequently colonizes 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). It is therefore likely that our sampling threshold of >19 cm dbh resulted in a conservative estimate of *Ips*-caused tree mortality, especially on C and T, where the confounding effect of prescribed burns was absent. In some areas, top killing of pines by *Ips* spp. is common (Furniss and Carolin 1977), but this was not evident in our study.

Bark Beetle-Caused Tree Mortality—Fir FE

The FE colonizes 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 (Ferrell 1980). A total of 1,098 white firs (5.8% of all white fir) were colonized by FE among all experimental units. During the initial sample period, we observed a significant treat-

ment effect in the amount of FE-caused tree mortality for all dbh classes combined ($F_{3,8} = 5.0$, $P = 0.03$) and within the two smallest dbh classes ($P < 0.015$, both cases). In the smallest dbh class, significantly higher levels of FE-caused tree mortality occurred on T+B than on C or T (Fig. 5A); however, significantly higher levels occurred on B than on any other treatment in the 34.3 cm dbh class (Fig. 5A). For all dbh classes combined, significantly higher levels of tree mortality occurred on T+B than on T (Fig. 5A). Mean

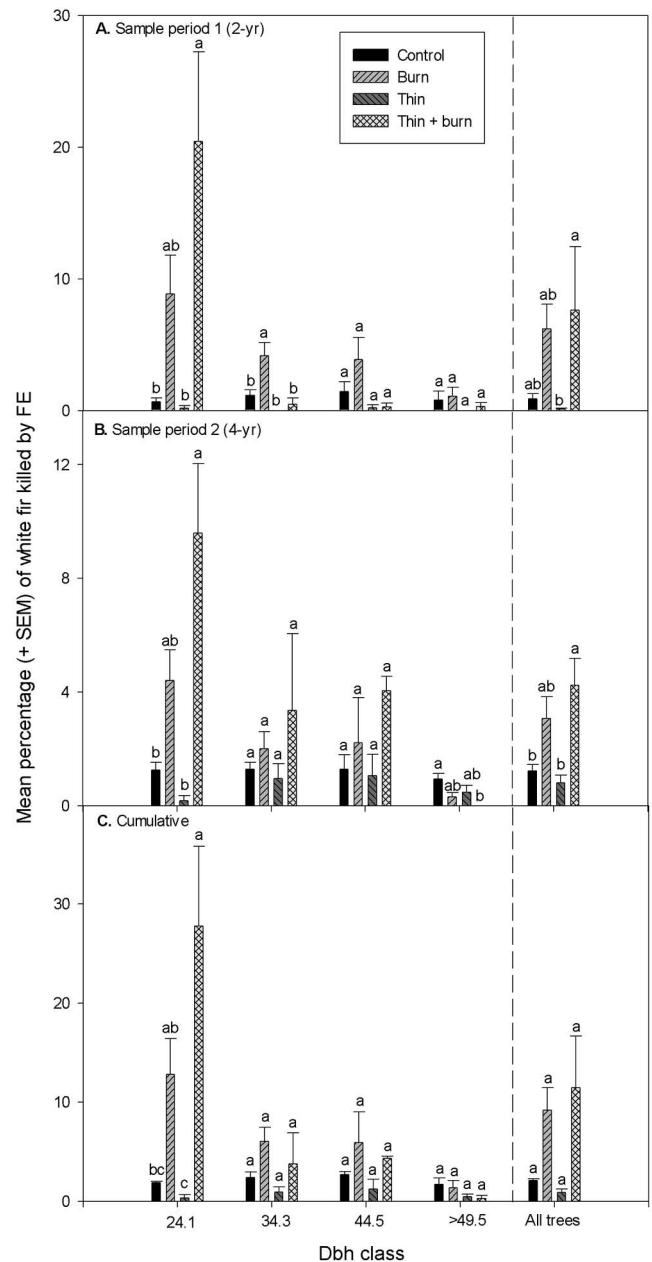


Figure 5. Mean percentage of white firs killed by FE (*S. ventralis*) by diameter class (midpoint of 10-cm diameter classes shown except for largest diameter class) for evaluations completed 2 years (A, sample period 1), 4 years (B, sample period 2), and cumulatively (C, sample periods 1 + 2) after prescribed burns were implemented, Southern Cascades site, Klamath National Forest, California. Treatments included: (1) untreated control—no manipulation, (2) burn—prescribed burned in fall, (3) thin—thinned from below, and (4) thin + burn. Means (+ SEM) followed by the same letter within groups are not significantly different ($P > 0.05$).

levels of bark beetle-caused tree mortality ranged from <1% (several treatments) to 20.4% (T+B, smallest dbh class).

During the second sample period, we also observed a significant treatment effect for all dbh classes combined ($F_{3,8} = 6.4$, $P = 0.016$) and for the smallest and largest dbh classes ($P < 0.029$, both cases). Significantly higher levels of FE-caused tree mortality occurred on T+B than on C or T in the smallest dbh class and for all dbh classes combined (Fig. 5B). Higher levels occurred on C than on T+B in the >49.5 cm dbh class (Fig. 5B). Mean levels of bark beetle-caused tree mortality ranged from 0% (T+B, largest dbh class) to 9.6% (T+B, smallest dbh class). Cumulatively, a significant treatment effect was observed only for the smallest dbh class ($F_{3,8} = 15.1$, $P = 0.001$) (Fig. 5C). Significantly higher levels of FE-caused tree mortality occurred on T + B than on C or T (Fig. 5C), and on B than on T (Fig. 5C). Mean levels of bark beetle-caused tree mortality ranged from <1% (T) to 27.8% (T+B). Approximately 85.2% (936 trees) of all FE-caused tree mortality occurred on experimental units that were prescribed burned (B and T+B).

In recent years, the body of literature concerning bark beetle responses to vegetation management treatments in ponderosa pine forests has increased substantially (reviewed by Parker et al. 2006, Fettig et al. 2007). However, surprisingly few studies have detailed effects in true fir forests or on the fir component within mixed-conifer forests. Schwilke et al. (2006) found that the probability of FE attack and associated levels of tree mortality were greater for smaller diameter firs after prescribed fire in the central Sierra Nevada. Attacks were more frequent after early season burns than after late season burns. Fettig et al. (2008) reported that applications of prescribed fire resulted in a significant increase in the proportion of white firs killed by FE and that mortality was concentrated in the smaller diameter classes. Filip et al. (2007) examined causes of tree mortality after a mixed-severity wildfire in a mixed-conifer forest in central Oregon. Two years after the fire approximately 20% of grand firs (*Abies grandis* [Dougl. ex D. Don] Lindl.) with 10–30% bole scorch that were alive the year after the fire were killed by FE. Again, higher levels of mortality were observed in smaller diameter firs in their study.

RTB

RTB colonizes all species of pine within its native range and occasionally fir, spruce (*Picea* spp.), and larch (*Larix* spp.). Attacks are usually confined to basal portions of previously stressed, weakened, or dead and dying trees or those under attack by other bark beetles, such as WPB (Fettig et al. 2004a). It is well established that RTB colonizes fire-injured trees, yet the species is rarely considered to be an important cause of tree mortality (Furniss and Carolin 1977, Parker et al. 2006), except in China where RTB was accidentally introduced (Li et al. 2001). During the first sample period, approximately 73.6% (218 trees) and 15.2% (45 trees) of bark beetle-killed pines contained evidence of RTB attacks on B and on B+T, respectively. Higher numbers of attacks occurred on individual trees on B

(9.5 ± 2.2 , mean $\pm$ SEM), T (28.3 ± 23.4), and T+B (9.8 ± 3.6) than on C (6.4 ± 1.2) during the first sample period ($F_{3,8} = 8.2$, $P = 0.008$). No other significant differences were observed among treatments during the first sample period. The high density of RTB attacks on T is an artifact of the data as only one RTB-attacked tree was recorded on each of three replicates (3 trees), one of which had 75 attacks.

It is possible for RTB populations to increase in fire-injured pines and attack adjacent apparently healthy trees (e.g., Ganz et al. 2003; Fettig et al. 2004a, 2006, 2008) or predispose trees to attack by other bark beetle species (Bradley and Tueller 2001). However, the percentage of bark beetle-killed pines that contained evidence of RTB attacks substantially declined on B (23.1%, 66 trees) during the second sample period. No significant treatment effect was observed during the second sample period ($F_{3,8} = 1.7$; $P = 0.25$). Fettig et al. (2008) reported >98% of pines that were attacked by RTB occurred on split plots that had been prescribed burned, but no tree mortality was attributed to these attacks.

Wood Borers

Some wood borers (Coleoptera: Buprestidae, Cerambycidae) are attracted to fire (Evans 1966), smoke (Wickman 1964), and fire-injured trees (Rasmussen et al. 1996), but their contribution to tree mortality, although thought to be rare (DeNitto et al. 2000, Parker et al. 2006), is largely unknown (Rasmussen et al. 1996, Fettig et al. 2008). Some species are regarded as forest pests. For example, California flatheaded borer (*Melanophila californica* Van Dyke) is known to cause tree mortality, particularly during extended periods of drought (Furniss and Carolin 1977). In Montana, fire-weakened Douglas-fir and western larch (*Larix occidentalis* Nutt.) were killed by wood borers, primarily the flatheaded fir borer (*Melanophila drummondi* [Kirby]), up to 1 year after a mixed-severity wildfire (Ken Gibson, pers. comm., Forest Health Protection, Mar. 23, 2007). McHugh et al. (2003) reported that wood borers were the most common insects found in ponderosa pine after mixed-severity wildfires and prescribed burns in northern Arizona.

Fettig et al. (2008) reported that wood borer attacks directly contributed to tree mortality in numerous fire-injured trees 2 years after the application of prescribed fires in northern California and that in the absence of such attacks tree mortality would probably not have occurred. At Southern Cascades, we observed only 15 and 17 trees (pine and fir) on B and T+B, respectively, that were currently fading (i.e., had died within the last year) and contained wood borers only (i.e., presence of primary bark beetles was not evident in portions of the bole that were examined) during the initial sample period, suggesting that mortality was therefore partially attributable to wood borer attacks. However, 18.5% of the pines (five trees) also contained large numbers of RTB attacks (≥ 30 attacks/tree, maximum = 83), which is a confounding factor. Only three trees met these conditions during the second sample period. There was no evidence of wood borers directly contributing to tree mortality on C and T. Although a body of literature is

building concerning evidence of wood borers directly contributing to tree mortality in fire-injured trees (Parker et al. 2006, Fettig et al. 2008), they were not an important source of tree mortality in this study.

Tree Diameter

Several studies have reported that bark beetle colonization rates are positively correlated with tree diameter, particularly in ponderosa pine (Fettig et al. 2007). However, we found diameter had no influence on colonization rates for MPB, WPB, FE, and all bark beetle species combined on C where no manipulation occurred ($df = 3, 8; P > 0.41$, all cases). However, we did observe significantly higher rates of tree mortality (i.e., pooled across all treatments) attributed to MPB, FE, and all bark beetle species combined in the smallest dbh class compared to the largest dbh class ($df = 3, 43, P < 0.028$, all cases) (Fig. 6).

Generally, larger trees are more fire-resistant (Peterson and Ryan 1986, Harrington 1993, Thies et al. 2005). However, larger trees 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, and reduced tree vigor, especially during drought (McHugh and Kolb 2003). 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 postfire mortality in ponderosa pine with increasing tree diameter and height. Fire-injured trees that do not die directly from prescribed fire (those detailed in this study) are generally more susceptible to bark beetle attacks (Parker et al. 2006). As discussed previously, MPB frequently colonizes smaller diameter ponderosa pines in California, whereas WPB attacks are

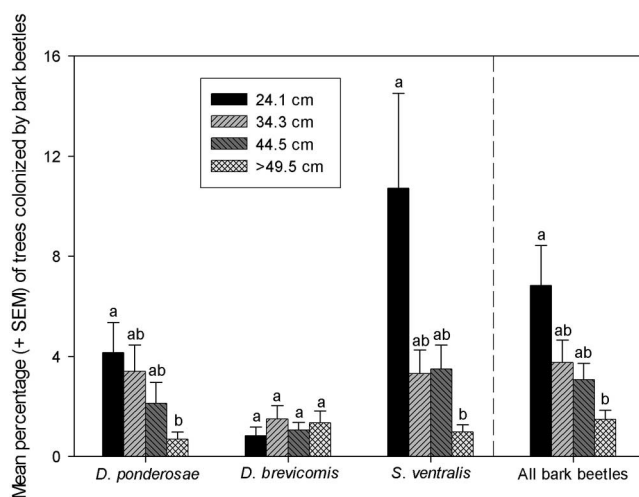


Figure 6. Mortality of all available trees among diameter classes (midpoint of 10-cm diameter classes shown except for largest diameter class) attributed to MPB (*D. ponderosae*), WPB (*D. brevicomis*), FE (*S. ventralis*), and all bark beetle species pooled across all treatments, Klamath National Forest, California. Means (+ SEM) followed by the same letter within groups are not significantly different ($P > 0.05$).

concentrated in the larger diameter classes (Miller and Keen 1960), which probably explains the different effects observed for these species (Fig. 6).

Some authors have stated that older ponderosa pines are more susceptible to mortality after fire than younger, mature trees (Kolb et al. 2007). For example, McHugh and Kolb (2003) reported mortality 3 years after fire was highest for trees with the smallest diameters (<20 cm dbh), which agrees with our study. Mortality decreased as diameter increased between 20 and 50 cm dbh as would be expected due to increasing bark thickness. However, mortality increased as diameter increased among the largest trees (>50 cm dbh) in their study. Similarly, Fulé et al. (2002) reported 67% of large-diameter (>50 cm dbh) ponderosa pines died within 2 years after prescribed burns compared with 19% mortality for smaller diameter trees. Other studies have reported similar trends described as a “U-shaped” distribution of ponderosa pine mortality by tree diameter (Kolb et al. 2007), which disagree with our results. However, our data are limited to delayed mortality attributable to bark beetle attack (i.e., it excludes trees directly killed by prescribed burns) in trees >19 cm dbh.

Stand Density

Fettig et al. (2007) provide a review of tree and stand factors associated with bark beetle infestations and discuss mechanistic explanations on the effectiveness of reducing stand density for preventing bark beetle infestations. Factors such as basal area and stand density index are consistently identified as primary attributes associated with bark beetle infestations. Craighead (1925) and Miller (1926) were among the first to demonstrate that slower growing ponderosa pines were more susceptible to WPB attack. Further investigations (Person 1928, 1931) led to development of a classification system for rating ponderosa pine susceptibility to WPB (Keen 1936). Since that time, a considerable amount of effort has been devoted to the identification of tree and stand conditions associated with bark beetle attacks in western coniferous forests.

We found no relationship between basal area (m^2/ha) or stand density index (SDI) and the percentage of trees killed by bark beetles. However, there was a significant correlation between trees/ha and percentage of trees killed by bark beetles (Table 2, Fig. 7). We also found significant correlations between the percentage of pines killed by bark beetles and basal area (m^2/ha), trees/ha, and SDI (Table 2; Fig. 8A–C). Trees/ha best predicted the amount of pine mortality attributed to bark beetles ($r^2 = 0.76$) (Fig. 8B). No significant correlations were found between measures of

Table 2. Correlations between three measures of stand density and the percentage of trees killed by bark beetles, Southern Cascades site, Klamath National Forest

Stand density variables	All trees ¹	<i>Pinus</i> only	<i>Abies</i> only
Basal area (m^2/ha)	0.422	0.675*	−0.191
Trees/ha	0.636*	0.869*	−0.073
SDI	0.526	0.770*	−0.144

¹ Values are Pearson's correlation coefficients (r), $n = 12$.

* Significance at $P = 0.05$.

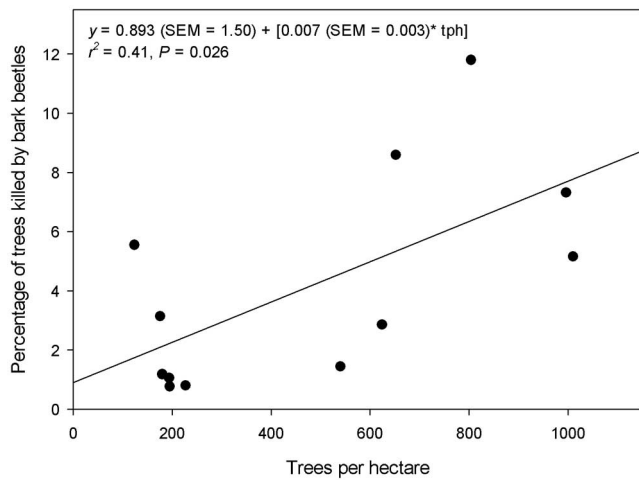


Figure 7. Relationship between numbers of trees (tph, trees/ha) and percentage of trees killed by bark beetles pooled across all treatments ($n = 12$), Klamath National Forest, California.

stand density and the percentage of trees killed by FE (Table 2). These analyses included data from all experimental units ($n = 12$; $df = 1, 10$). We also sorted data by the presence of prescribed burns (burned = B and T+B, unburned = C and T; $n = 6$; $df = 1, 4$) and repeated these analyses for each group. For each of 18 analyses, we reached the same statistical conclusions with the exception that trees/ha was not significantly correlated with the percentage of trees killed by bark beetles on burned units ($P = 0.081$), SDI was significantly correlated with the percentage of trees killed by bark beetles on unburned units ($r = 0.88$; $P = 0.022$), and basal area was not significantly correlated with the percentage of pines killed by bark beetles on unburned units ($P = 0.122$). The consistency of these results is surprising, given differences in the level of replication and the influence of prescribed burns on tree susceptibility to bark beetle attack.

Several studies have demonstrated that stand density is positively correlated with MPB and roundheaded pine beetle (*Dendroctonus adjunctus* Blandford) infestation levels in ponderosa pine forests (e.g., Negrón 1997, Negrón et al. 2000, 2008; Negrón and Popp 2004, Kolb et al. 2007). Sartwell and Stevens (1975) examined 44 groups of MPB infestations in the Black Hills of South Dakota and concluded that stands containing $>34.4 \text{ m}^2/\text{ha}$ of basal area were more susceptible to MPB infestation. At Southern Cascades, our model predicts a pine loss of about 4% at this density (Fig. 8A). 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 $<9 \text{ m}^2/\text{ha}$ of basal area, which agrees with the optimal stocking level of $11 \text{ m}^2/\text{ha}$ described by Oliver (1979, 1995) and our model predictions. Furthermore, Oliver (1995) reported that maximum SDI for even-aged ponderosa pine stands in northern California was regulated by MPB and WPB infestations. A SDI value of 230 defined a threshold for a zone of imminent bark beetle-caused tree mortality within which endemic populations kill a few trees, but net growth is positive.

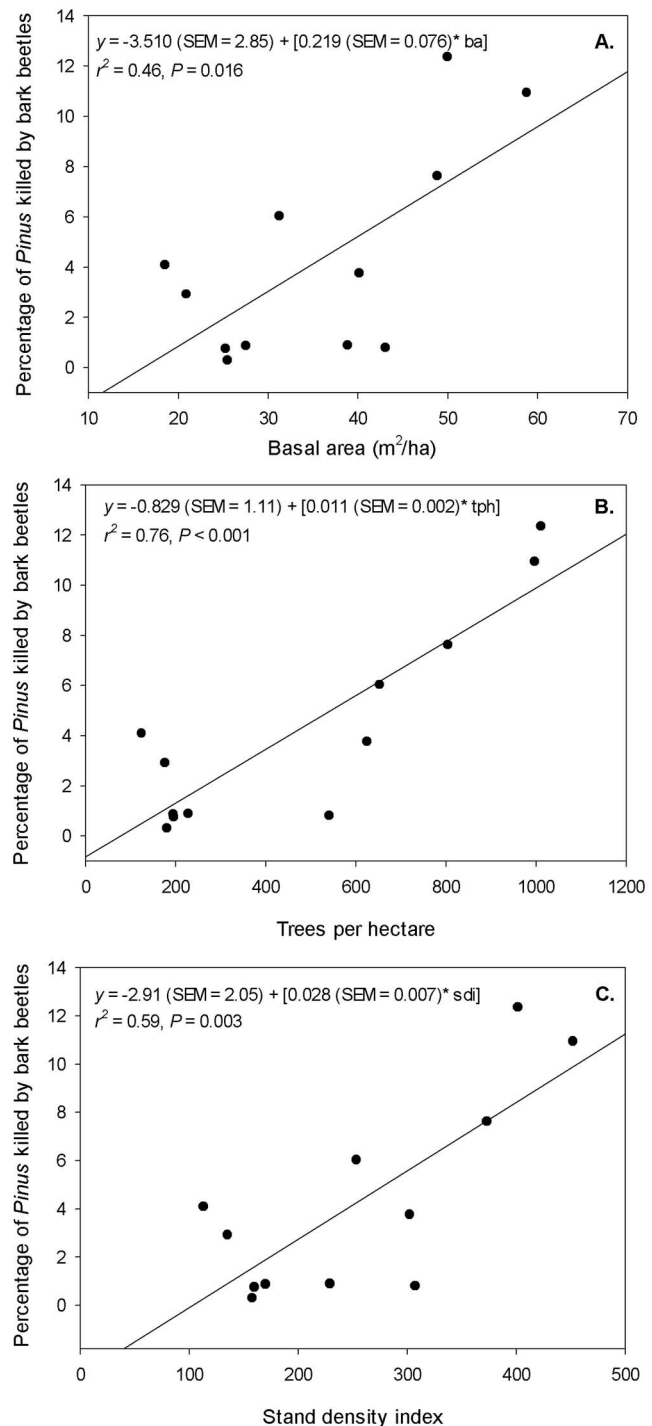


Figure 8. Relationship between (A) basal area (ba, m^2/ha), (B) numbers of trees (tph, trees/ha), (C) SDI, and percentage of pines killed by bark beetles pooled across all treatments ($n = 12$ for each analysis), Klamath National Forest, California.

Maximum SDI was defined as 365. Oliver stated 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. In our study, SDI explained less of the variation in the percentage of pines killed by bark beetles than trees/ha but was a better predictor than basal area (Fig. 8A–C). Three experimental units, in which bark beetle-caused tree mortality averaged 10.3% for pine and 8.1% for all trees, had SDI values of >365 . On experimental units

with SDI values <365 SDI, mortality averaged 2.3 and 2.8% for pine and all trees, respectively. Despite the lack of any statistically significant differences in the amount of bark beetle-caused tree mortality between T and C (see above), these analyses further support the value of managing stand density for reducing stand susceptibility to bark beetle attack (Figs. 7 and 8A–C).

Few data are available on stand factors associated with bark beetle infestations in true fir forests. McMillin et al. (2003) related the extent of subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) mortality caused by western balsam bark beetle (*Dryocoetes confusus* Swaine) to forest conditions in Wyoming. Significant positive linear relationships were found between amount of fir mortality and percentage of subalpine fir trees, subalpine fir basal area, and subalpine fir SDI. Ferrell et al. (1994) reported a significant linear relationship between FE-caused tree mortality and white fir basal area during a widespread outbreak that occurred during an extended drought in the Lake Tahoe Basin, California. We found no such relationship under the conditions of this study (Table 2). A risk rating system that uses crown and bole characteristics is available for predicting the probability of individual tree mortality for red and white fir in northern California (Ferrell 1980).

Thinning affects not only the vigor of residual trees but also the physical environment within treated stands (Fettig et al. 2007). Increased temperatures and wind speeds are common within thinned stands and may accelerate the development of certain bark beetle species and force them to overwinter in stages that are more susceptible to freezing (Amman 1973) or cause turbulences that disrupt pheromone plumes used for recruiting conspecifics during initial phases of host tree colonization (Thistle et al. 2004). Our surveys were conducted several years after treatments were implemented (Table 1), which was sufficient to fully influence abiotic conditions but may not be sufficient to allow certain trees to fully capture the new growing space that has been allocated to them. Generally, the positive effects of vegetation management treatments on resource uptake and tree growth in ponderosa pine occurs shortly (usually within 1 year) after treatment (e.g., Kolb et al. 1998, Stone et al. 1999, Wallin et al. 2004, 2008; Sala et al. 2005, Skov et al. 2005, Zausen et al. 2005) and although little evidence of thinning shock exists in ponderosa pine, the onset of increased growth may be delayed for 5–25 years after thinning in some trees (Kolb et al. 2007). Accordingly, significant differences in the amount of bark beetle-caused tree mortality between C and T may be observed in the future.

Time Since Treatment

Some authors have expressed concerns about the potential for bark beetle populations to increase in fire-affected trees and subsequently colonize apparently healthy trees (Parker et al. 2006). Large numbers of severely stressed trees provide abundant host material, and once this resource has been exhausted (i.e., within 1–2 years after prescribed burns), bark beetles may attack and kill trees that might otherwise have survived. Overall, the amount of bark beetle-caused tree mortality was almost evenly distributed be-

tween surveys, with 53.8% (979 trees) recorded during the first sampling period. No significant differences were found with regard to the amount of bark beetle-caused tree mortality occurring 2 and 4 years after the application of prescribed burns for all dbh classes combined or within individual dbh classes ($df = 1, 22, P > 0.14$, all cases) (Fig. 9A). This result is surprising, given the relationship between burn severity and tree susceptibility to bark beetle attack (see above), which we hypothesized would result in significantly higher levels of bark beetle-caused tree mortality during the first sample period. For example, Breece et al. (2008) reported that approximately 80% of all bark beetle-attacked trees were colonized during the first year after the application of prescribed burns. Eight and 12% were colonized during the second and third years, respectively. Accordingly, we conducted further analyses using data from prescribed burned units (B and T+B). Only one of five analyses yielded a significant effect ($F_{1,10} = 7.12, P = 0.024$) (Fig. 9B), in which significantly higher levels of bark beetle-caused tree mortality occurred 2 years after the application of prescribed fire in the smallest dbh class. No significant differences were found with regard to the amount of bark beetle-caused tree mortality in C between the two surveys ($df = 1, 4, P > 0.18$, all cases).

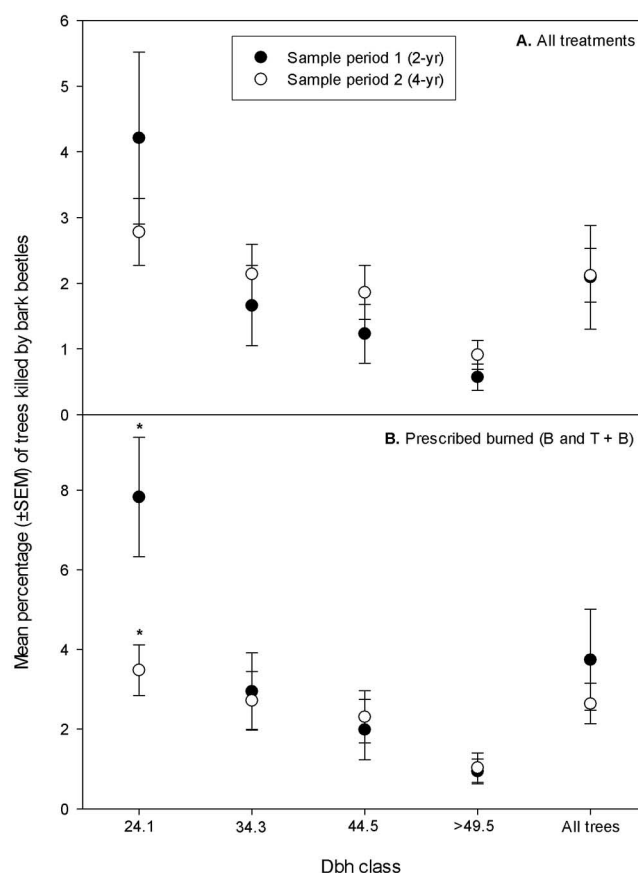


Figure 9. Mean percentage of trees killed by bark beetles by sample period (i.e., time since application of prescribed burns) for (A) all treatments or (B) those that were prescribed burned by diameter class (midpoint of 10-cm diameter classes shown except for largest diameter class), Klamath National Forest, California. *Significant difference between treatments.

Conclusions

The intended focus for GAMA, as stated in the Northwest Forest Plan Record of Decision, is “Development of ecosystem management approaches, including use of prescribed burning and other silvicultural techniques, for management of pine forests, including objectives related to forest health, production and maintenance of late-successional forest and riparian habitat, and commercial timber production” (USDA and USDI 1994). The primary objective of the FFS study at Southern Cascades was to create stand conditions that serve as a model of resiliency to wildfire (i.e., the “80/80 rule”; McIver and Weatherspoon 2009) while being guided by a desired future condition consistent with shifting stand composition from fir to pine and increasing residual tree size. Accelerating the growth of younger trees by thinning and prescribed burning has been recommended to promote more rapid development of old-growth stand conditions in ponderosa pine forests (Covington et al. 1997, Kolb et al. 2007), but the creation of such conditions will take decades and therefore maintenance of existing stocks of large trees is critical. In general, little information exists on the response of older, larger trees to such treatments (Kolb et al. 2007).

A total of 1,822 pine and fir trees (5.1% of all trees) were killed by bark beetles, which represents the loss of about 15 trees/ha across all experimental units. Significantly higher rates of bark beetle-caused tree mortality occurred on B (9.2%) than on C (3.2%), T (<1%), or T+B (3.3%) during the first sample period. A total of 723 pines (4.4% of all pines) were colonized by bark beetles. Significantly higher levels of pine mortality were attributed to bark beetles on B (5%) than on C, T, or T+B (all <1%) during the first sample period, of which about 50.9% (368 trees) occurred on B. Despite the lack of statistically significant differences between C and T during the course of this study, correlation and regression analyses of stand density measures provide further evidence supporting the value of thinning for reducing pine susceptibility to bark beetle attack.

Treatment B may interfere with management objectives as the delayed mortality within the pine component may be too great. However, much of the mortality was concentrated in the smaller diameter classes (e.g., 183 versus 28 for smallest and largest dbh classes, respectively). Treatments T and T+B had relatively little bark beetle-caused tree mortality, except in reference to the fir component. However, our objective was to promote pine over fir and little FE-caused tree mortality occurred in the larger diameter classes (e.g., 44 versus 1 for smallest and largest dbh classes in T+B, respectively). Our desired future condition included maintenance of large-diameter trees regardless of tree species. Accordingly, T and T+B seem effective in meeting both fuel reduction and forest restoration objectives. We found no strong evidence that bark beetle populations increased in fire-injured trees during the first 2 years after the application of prescribed fire and subsequently colonized adjacent apparently healthy trees.

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