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Thinning Jeffrey pine stands to reduce susceptibility to bark beetle infestations in California, U.S.A.

Christopher J. Fettig, Christopher J. Hayes, Karen J. Jones∗, Stephen R. Mckelvey, Sylvia L. Mori† and Sheri L. Smith‡

*Pacific Southwest Research Station, USDA Forest Service, Davis, CA 95618, U.S.A., *Tahoe National Forest, USDA Forest Service, Foresthill, CA 95631, U.S.A., †Pacific Southwest Research Station, USDA Forest Service, Berkeley, CA 94701, U.S.A., and ‡Forest Health Protection, USDA Forest Service, Susanville, CA 96130, U.S.A.*

Abstract

1 Bark beetles (Coleoptera: Curculionidae, Scolytinae) are commonly recognized as important tree mortality agents in coniferous forests of the western U.S.A.

2 High stand density is consistently associated with bark beetle infestations in western coniferous forests, and therefore thinning has long been advocated as a preventive measure to alleviate or reduce the amount of bark beetle-caused tree mortality.

3 The present study aimed to determine the effectiveness of thinning to reduce stand susceptibility to bark beetle infestations over a 10-year period in *Pinus jeffreyi* forests on the Tahoe National Forest, California, U.S.A. Four treatments were replicated three times within 1-ha square experimental plots. Treatments included thinning from below (i.e. initiating in the smallest diameter classes) to a residual target basal area (cross-sectional area of trees at 1.37 m in height) of: (i) 18.4 m^2/ha (low density thin); (ii) 27.6 m^2/ha (medium density thin); (iii) 41.3 m^2/ha (high density thin); and (iv) no stand manipulation (untreated control).

4 Throughout the present study, 107 trees died as a result of bark beetle attacks. Of these, 71% (75 trees) were *Abies concolor* killed by *Scolytus ventralis*; 20.6% (22 trees) were *Pinus ponderosa* killed by *Dendroctonus ponderosae*; 4.7% (five trees) were *P. jeffreyi* killed by *Dendroctonus jeffreyi*; 1.8% (two trees) were *P. jeffreyi* killed by *Ips pini*; 0.9% (one tree) were *P. jeffreyi* killed by *Orthotomicus* (= *Ips*) *latidens*; 0.9% (one tree) were *P. ponderosa* killed by both *Dendroctonus brevicomis* and *D. ponderosae*; and 0.9% (one tree) were *P. jeffreyi* killed by unknown causes.

5 In the low density thin, no pines were killed by bark beetles during the 10-year period. Significantly fewer trees (per ha/year) were killed in the low density thin than the high density thin or untreated control. No significant treatment effect was observed for the percentage of trees (per year) killed by bark beetles.

Keywords *Dendroctonus brevicomis*, *Dendroctonus jeffreyi*, *Dendroctonus ponderosae*, *Ips*, *Pinus jeffreyi*, *Pinus ponderosa*, Scolytinae, silviculture.

Introduction

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are commonly recognized as important tree mortality agents in coniferous forests of the western U.S.A. (Furniss & Carolin, 1977). Many bark beetle species feed on the phloem tissue of woody plants, often directly killing the host, and influencing forest ecosystem structure and function by regulating certain aspects of primary production, nutrient cycling and ecological succession, as well as the size, distribution and abundance of forest trees (Mattson *et al*., 1996). Attacks may reduce tree growth and cause mortality and subsequent replacement by other tree species. In the western U.S.A., bark beetle outbreaks impact timber and fibre production; water quality and quantity; fuel loadings; fish and wildlife habitat and populations; recreation; grazing capacity; real estate values; biodiversity; carbon storage; endangered species; and cultural resources.

High stand density is consistently associated with bark beetle infestations in western coniferous forests (Fettig *et al*., 2007).

Correspondence: Christopher J. Fettig. Tel.: +1 530 759 1708; fax: +1 530 747 0241; e-mail: cfettig@fs.fed.us

Craighead (1925) and Miller (1926) were among the first to demonstrate that slower growing trees were more susceptible to bark beetle attacks. Further investigations (Person, 1928, 1931) led to development of a classification system for rating ponderosa pine *Pinus ponderosa* Dougl. ex Laws. susceptibility to western pine beetle, *Dendroctonus brevicomis* LeConte attacks (Keen, 1936). Subsequently, a considerable amount of effort has been devoted to the identification of tree and stand conditions associated with bark beetle infestations (Fettig *et al*., 2007), most of which, in the western U.S.A., has concentrated on effects in *P. ponderosa* and lodgepole pine *Pinus contorta* Dougl. ex Loud. forests.

Thinning has long been advocated as a preventive measure to alleviate or reduce the amount of bark beetle-caused tree mortality in western coniferous forests (Wood *et al*., 1985; Whitehead *et al*., 2004; Whitehead & Russo, 2005; Fettig *et al*., 2007). Thinnings conducted in a careless manner may, however, also result in physical damage to residual trees, soil compaction and increased rates of windthrow. Although thinning may reduce tree and stand susceptibility to bark beetle attack, there may be elevated potentials for increases in subcortical insects and root pathogens (Harrington *et al*., 1985). With knowledge of these potential risks, prudent silvicultural treatments can be implemented to minimize potential unwanted consequences. Fettig *et al*. (2007) reviewed tree and stand factors associated with bark beetle infestations, and provided mechanistic explanations on the effectiveness of thinning for preventing bark beetle infestations. In their work, they identified several forest cover types and bark beetle species for which little or no data were available, including Jeffrey pine *Pinus jeffreyi* Grev. & Balf. forests.

Pinus jeffreyi ranges from the Klamath Mountains in northwestern California and southwestern Oregon, U.S.A., throughout much of the Sierra Nevada, U.S.A., to the Transverse and Peninsular Ranges of Southern California, and the Sierra San Pedro Mártir of Baja California, Mexico (Jenkinson, 1990). The type occupies >81 000 ha and is dominant in forests east of the Sierra Nevada crest, and in the Transverse and Peninsular Ranges. In much of this region, highly-effective fire suppression and differential cuttings of large-diameter, fire-tolerant tree species, such as *P. jeffreyi*, resulted in substantial changes in the structure and composition of forests over the last 150 years. Open park-like forests of widely-dispersed *P. jeffreyi* were once common, and maintained by frequent thinning of small-diameter trees and fire-intolerant tree species by low-intensity surface fires, as well as competitive exclusion of tree seedlings by understory grasses.

In general, *P. jeffreyi* is more cold hardy and drought tolerant than many of its common associates and therefore competes well on cold, xeric and relatively infertile sites where growth rates are approximately half those found on the western slope of the Sierra Nevada (Helms, 1995). The Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins, is the major bark beetle pest of *P. jeffreyi* and, under endemic conditions, usually attacks individual mature trees. During epidemics, however, group kills of 20–30 trees are common and trees >10 cm dbh diameter at breast height (dbh; 1.37 m in height on the tree bole) may be attacked and killed (Smith *et al*., 2009). Smith *et al*. (2009) reviewed the life history and management of *D. jeffreyi*, a species that has been understudied compared with many of its bark beetle associates (e.g. *D. brevicomis*).

In much of the Sierra Nevada, *P. jeffreyi* grows in close association with *P. ponderosa* and white fir *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. *Dendroctonus brevicomis* is a major cause of *P. ponderosa* mortality throughout much of the western U.S.A., and particularly in California. Under certain conditions, such as extended drought, *D. brevicomis* can attack and kill apparently-healthy trees of all ages and size classes (Miller & Keen, 1960). The mountain pine beetle *Dendroctonus ponderosae* Hopkins also colonizes *P. ponderosa* and several other pines, most notably *P. contorta*, sugar pine *Pinus lambertiana* Dougl., whitebark pine *Pinus albicaulis* Engelm. and western white pine *Pinus monticola* Dougl. ex D. Don (Furniss & Carolin, 1977). The role of *D. ponderosae* in *P. ponderosa* in California is often secondary to that of *D. brevicomis* (Miller & Keen, 1960), particularly in larger diameter trees. Fir engraver *Scolytus ventralis* LeConte is the major bark beetle pest of true firs, particularly *A. concolor*. Trees of all sizes may be attacked and killed, although outbreaks are typically associated with trees stressed by drought, defoliation or other factors (Ferrell *et al*., 1994). Other common associates of *P. jeffreyi* include incense cedar *Calocedrus decurrens* (Torr.) Florin, *P. contorta*, *P. lambertiana*, *P. monticola* and California red fir *Abies magnifica* A. Murr. (Jenkinson, 1990). All of these tree species may be attacked and killed by bark beetles (Furniss & Carolin, 1977), although mortality of *C. decurrens* as a result of bark beetle attack is rare.

The present study aimed to determine the effect of thinning, conducted specifically for reducing stand susceptibility to bark beetle infestations, in *P. jeffreyi* forests on subsequent levels of bark beetle-caused tree mortality over a 10-year period.

Materials and methods

Study site and treatments

In June 1997, 12 1-ha square experimental plots were established in a second-growth stand located on the Truckee Ranger District, Tahoe National Forest, California (39.47°N, 120.05°W; mean elevation = 2088 m a.s.l.). The climate of the study site is characterized by hot summers [average maximum temperature (June to September) = 26.2 °C] with little precipitation [average total precipitation (June to September) = 60 mm] and cool winters [average maximum temperature (December to March) = 6.8 °C]. Annual precipitation averages 568 mm, with the majority coming in the form of snow [average annual snowfall = 2619 mm; Western Regional Climate Center, Reno, Nevada; Boca (9.7 km south-south-west of study site, elevation = 1701 m a.s.l.)]. The associated climate and thin soils combine for low site quality. The study area was initially logged in the mid to late 1800s and regenerated naturally (K. J. Jones, unpublished data). After decades of highly-effective fire suppression, there were substantial changes in the structure and composition of these forests including large increases in the abundance of *A. concolor*.

One of four treatments was randomly assigned to each plot and replicated three times. Treatments included thinning from below (i.e. initiating in the smallest diameter classes) to a residual target basal area (cross-sectional area of trees at 1.37 m in height) of: (i) 18.4 m^2/ha with 7.3 m average spacing (low density thin); (ii) 27.6 m^2/ha with 6.1 m average spacing (medium density thin); (iii) 41.3 m^2/ha with 4.9 m average spacing (high density thin); and (iv) no stand manipulation (untreated control) (Table 1). *Pinus jeffreyi* was favoured for retention over other tree species when residual density and spacing criteria were met. There were no other tree species preferences. Additionally, trees of good form that were void of apparent insect and disease infestations and mechanical damage were selected for retention. Leave trees had >30% live crown ratios and all snags not creating a hazard were retained. Logging was conducted via a commercial timber sale in 1998. Special care was taken to avoid mechanical damage to residual trees, or excess soil disturbance and compaction. Slash removal and treatment of submerchantable materials was accomplished by USDA Forest Service timber management personnel in 1999. All submerchantable trees, regardless of species, were cut and removed to a central location with all terrain vehicles, where they were piled for disposal. After thinning, stand density on an individual plot basis was in the range of 156–539 trees/ha, and 18.6–39.3 m^2/ha of basal area (Table 1). In the low and medium density thin plots, *P. jeffreyi* was the dominant (based on number of trees) tree species, whereas, in the high density thin and untreated control, *P. ponderosa* was dominant.

A 100% survey was conducted on each experimental plot ($n = 12$) to locate dead and dying trees by presence of crown fade. Although some preliminary surveys were conducted, detailed cruises were first conducted in 2002 and annually thereafter. All recently killed trees >15 cm dbh containing successful bark beetle attacks (with oxidized phloem material present in pitch tubes and/or boring dust) were marked and tree species, bark beetle species and dbh recorded. A section of bark of approximately 625 cm^2 was removed with a hatchet at approximately 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, as well as host tree species, are commonly used to distinguish among bark beetle species (Furniss & Carolin, 1977). Bark removal also served as a means of separating tree mortality tallied during previous cruises. In some cases, deceased bark beetles were present beneath the bark, which helped confirm identifications based on gallery formation.

Experimental design and analysis

The primary variables of interest were the percentage of trees killed by bark beetles and the number of trees killed by bark beetles. The count of bark beetle-killed trees was assumed to have an over-dispersed Poisson distribution and its logarithm was regressed on the thinning treatment (low density, medium density, high density, untreated control), year (2002–2009) and plot effect (as a random effect to account for the repeated measurements) using the Poisson regression from the family of the generalized linear models (GLM) (McCulloch & Searle, 2001). The proportion of bark beetle-killed trees response was analyzed with an over-dispersed Logit model from the family of GLM. The counts of dead trees were assumed to have the binomial distribution from the population of trees alive at the beginning of the measuring year, and were regressed on the thinning treatment, year and plot effect (as a random effect to account for the repeated measurements). The estimation of all the parameters and the testing of multiple treatment pairwise comparisons were performed with the SAS GLIMMIX procedure (SAS Institiute, Cary, North Carolina), and the likelihood ratio

Table 1 Density and composition after thinning to reduce stand susceptibility to bark beetle infestations in *Pinus jeffreyi* stands, Tahoe National Forest, California, U.S.A.

Thinning treatment[a]	Residual[b] ba/ha	Residual[b] trees/ha	Stand density index[b]	% *Pinus jeffreyi*[c]	% *Pinus ponderosa*[c]	% *Abies concolor*[c]	% *Calocedrus decurrens*[c]
18.4 (low density)	21.6	158	142	65	12	21	2
18.4 (low density)	18.6	156	125	80	14	6	0
18.4 (low density)	24.1	183	159	36	51	3	10
Mean	21.4	166	142	60	26	10	4
27.6 (medium density)	26.6	284	188	68	25	7	0
27.6 (medium density)	25.0	235	173	64	28	4	4
27.6 (medium density)	28.9	294	202	48	35	12	5
Mean	26.8	271	188	60	29	8	3
41.3 (high density)	30.8	353	221	44	51	5	0
41.3 (high density)	39.0	296	258	40	30	27	3
41.3 (high density)	34.0	390	244	27	63	5	5
Mean	34.6	346	241	37	48	12	3
Untreated control	39.3	415	277	39	59	2	0
Untreated control	34.7	539	264	46	53	0	1
Untreated control	33.3	410	241	36	57	5	2
Mean	35.8	455	261	40	56	2	1

[a]Target residual tree density (basal area per ha; m^2/ha).
[b]Tree density measured after a commercial timber sale.
[c]Based on the number of trees.

test with the Bonferroni adjustment was used for multiple comparisons to attain an experiment-wise error rate of 0.05.

Results

Throughout the present study, 107 trees died as a result of bark beetle attacks (Table 2). Of these, 71% (75 trees) were *A. concolor* killed by *S. ventralis*; 20.6% (22 trees) were *P. ponderosa* killed by *D. ponderosae*; 4.7% (five trees) were *P. jeffreyi* killed by *D. jeffreyi*; 1.8% (two trees) were *P. jeffreyi* killed by pine engraver, *Ips pini* (Say); 0.9% (one tree) were *P. jeffreyi* killed by *Orthotomicus* (= *Ips*) *latidens*; 0.9% (one tree) were *P. ponderosa* killed by both *D. brevicomis* and *D. ponderosae*; and 0.9% (one tree) were *P. jeffreyi* killed by unknown causes (Table 2). The mean percentage of trees killed (all tree species) by bark beetles (per year) ranged from 0% [all thinned treatments (2005–2006), and medium and high density thin (2007)] to 1.2% [medium density thin (2002)] (Fig. 1). In 2005 and 2006, no bark beetle-caused tree mortality was observed in the thinned plots, regardless of the level of thinning, and only two trees died in the untreated control. The untreated control was the only treatment in which bark beetle-caused tree mortality was recorded in every year measured (Fig. 1). In the low density thin, no pines were killed by bark beetles throughout the 10-year period. Twenty-three *P. ponderosa* and *P. jeffreyi* were killed on untreated control plots compared with nine for all thinning treatments combined (Table 2).

No significant treatment effect was observed for the proportion of trees (all tree species) killed by bark beetles (per year) ($\chi^2 = 1.71$, $P = 0.63$) (Fig. 2A). However, significant treatment effects were observed for the number of trees killed by bark beetles (per ha/year) among treatments ($F_{3,21} = 6.39$, $P < 0.001$) (Fig. 2B) and among years ($F_{7,21} = 12.99$, $P < 0.001$). Fewer trees were killed in the low density thin than the high density thin ($\chi^2 = 9.98$, $P = 0.0016$) or untreated control ($\chi^2 = 14.28$, $P = 0.0002$) (Fig. 2B). No significant correlation was found between stand density (m^2/ha of basal area) and the number of trees killed by bark beetles when added in the models as a covariate. No significant differences were found among treatments for the proportion of *P. jeffreyi* (Fig. 3A), *P. ponderosa* (Fig. 3B) and *A. concolor* (Fig. 3C) killed by bark beetles. Overall, the highest percentage of tree mortality (per year) was observed for *A. concolor* in the untreated control, where $8.8 \pm 3.9\%$ (mean ± SEM) were killed by *S. ventralis* (Fig. 3C).

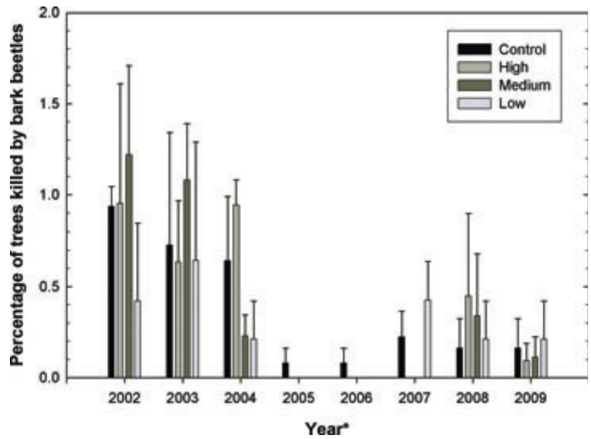

Figure 1 Percentage of trees killed by bark beetles after thinning [low (18.4 m^2/ha), medium (27.6 m^2/ha), high (41.3 m^2/ha), untreated control] in *Pinus jeffreyi* stands, Tahoe National Forest, California, U.S.A., 1999–2009. Bars represent the mean ± SEM (unpooled data used). *Data reported for 2002 include mortality occurring during the initial 3-years after treatment.

Discussion

In the present study, bark beetle-caused tree mortality was relatively low the decade after thinning, never reaching a level that would be considered epidemic for either *P. jeffreyi* or *P. ponderosa* (e.g. defined as >2% of trees killed per year; Hansen *et al*., 2006). Mortality was concentrated in *A. concolor*, whereas *P. jeffreyi*, our primary tree species of interest, experienced very low mortality (<0.2% per year). The low mortality reported in the present study, especially in the first few years after treatment, suggests that bark beetle-caused tree mortality was not exacerbated by tree damage (e.g. mechanical damage to residual trees) during the application of the thinning treatments. Tree mortality caused by *D. jeffreyi* was reported to be low on the Tahoe National Forest during much of this study (1999–2005, 2009; http://www.fs.fed.us/r5/publications/pestconditions) despite several years of below normal precipitation. In 2006–2008, however, levels of *D. jeffreyi*-caused tree mortality increased substantially in nearby areas on the Tahoe National Forest (http://www.fs.fed.us/r5/publications/pestconditions), although only three of the nine trees that were killed by *D. jeffreyi* in the present study were recorded during that time.

Table 2 Number of trees killed by bark beetles over a 10-year period after thinning (low density, medium density and high density) to reduce stand susceptibility to bark beetle infestations, Tahoe National Forest, California, U.S.A., 1999–2009

	Total number of trees killed by bark beetles (all bark beetle species)			
	Abies concolor	*Pinus ponderosa*	*Pinus jeffreyi*	All tree species
Low density	10	0	0	10
Medium density	20	5	0	25
High density	28	2	2	32
Untreated control	17	16	7	40
Total	75	23	9	107
Mean dbh[a]	31.1 (15–61)	28.4 (18–51)	26.0 (18–32)	30.1 (15–61)

[a]dbh (diameter at breast height, 1.37 m in height), range given in parentheses.

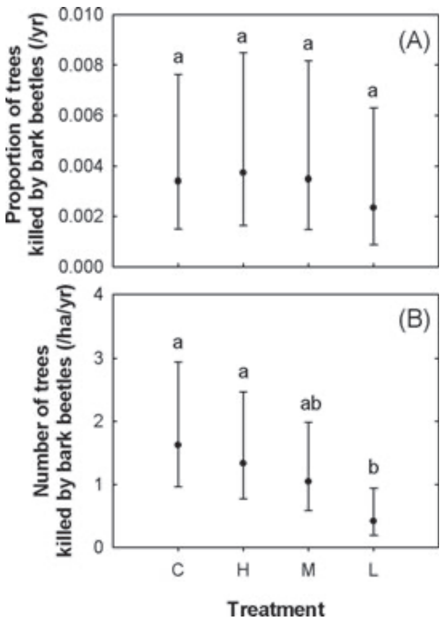

Figure 2 (A) Proportion of trees killed by bark beetles (per year) and (B) the number of trees killed by bark beetles (per ha/year) during a 10-year period after thinning [low (18.4 m^2/ha), medium (27.6 m^2/ha), high (41.3 m^2/ha), untreated control] in *Pinus jeffreyi* stands, Tahoe National Forest, California, U.S.A., 1999–2009. Points represent the mean with the 95% confidence interval. Bars followed by the same letter are not significantly different ($P > 0.05$).

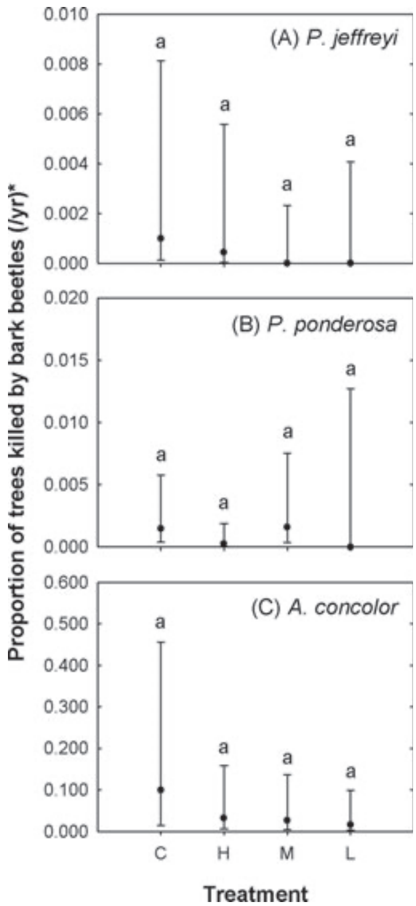

Figure 3 Proportion of (A) *Pinus jeffreyi*, (B) *Pinus ponderosa* and (C) *Abies concolor* trees killed by bark beetles (per year, all bark beetle species) over a 10-year period after thinning [low (18.4 m^2/ha), medium (27.6 m^2/ha), high (41.3 m^2/ha), untreated control] in *Pinus jeffreyi* stands, Tahoe National Forest, California, U.S.A., 1999–2009. Points represent the mean with the 95% confidence interval. Bars followed by the same letter are not significantly different ($P > 0.05$). *A theoretical upper confidence bound for the binomial distribution was calculated for treatments with zero mortality counts: Upper bound $= \frac{[1-0.05^{\frac{1}{ntrees}}]}{nyears}$.

Differences in bark beetle-caused tree mortality among thinning treatments were slight, although not unexpected considering that, with the exception of losses in *A. concolor* (a minor component in these stands; Table 1), bark beetle activity was low over the 10-year period (Fig. 1 and Table 2). Although we only observed one significant treatment effect in which significantly lower bark beetle-caused tree mortality (based on number of trees killed/ha/year) occurred on the low density thin compared with the high density thin and untreated control (Fig. 2B), we consider it important to reiterate that no pines were killed by bark beetles in the low density thin over the 10-year period (Fig. 1 and Table 2). We also note that when relative (percentage of trees) versus absolute (number of trees) levels of tree mortality are compared among treatments, large differences in total tree mortality and associated sources of brood production may be discounted. This is an important consideration for land managers who are concerned with limiting volume losses.

Although we took no direct measurements of tree vigour and thus cannot address this directly, the survival of all pines in our low density treatment suggests that thinning may have increased individual tree vigour. Colonization of live host trees by bark beetles requires overcoming tree defences consisting of anatomical and chemical components that are both constitutive and inducible (Wood, 1972; Raffa *et al*., 1993; Franceschi *et al*., 2005). In brief, this can only be accomplished by recruitment of a critical minimum number of beetles (Wood, 1972; Raffa *et al*., 1993), which varies with host vigour. Most conifers, particularly *P. jeffreyi* and *P. ponderosa*, have well-defined resin duct systems, which are capable of mobilizing large amounts of oleoresin after wounding. This is considered to be the primary defence of conifers against bark beetle attack (Vité & Wood, 1961; Reid *et al*., 1967; Smith, 1975). Beetles that initiate host colonization are often killed by drowning or immobilization in resin, especially when adequate moisture, resin flow and oleoresin exudation pressure exist (Vité & Wood, 1961). Resin chemistry may also play an important role (Reid *et al*., 1967; Smith, 1975). In the present study, some trees were observed to be attacked by bark beetles at levels insufficient to cause tree mortality.

Previous research has found high tree density to be associated with increased probability of bark beetle infestation in *P. ponderosa* (Negrón *et al*., 2000, 2008; Negrón & Popp, 2004; Hayes *et al*., 2009; Fettig *et al*., 2010), a tree species that grows in close association with *P. jeffreyi* in many locations. For example, Negrón and Popp (2004) established 35 clusters of *D. ponderosae*-infested and uninfested plots in *P. ponderosa* forests of north-central Colorado, U.S.A. Based on data collected from the plots, several classification models were developed for estimating the probability of infestation by *D. ponderosae*. The simplest model indicated a 50% greater probability of infestation when *P. ponderosa* basal area was >17.1 m^2/ha than when *P. ponderosa* basal area was ≤ 17.1 m^2/ha (Negrón & Popp, 2004). In the present study, only ten trees were killed by bark beetles in the low density thin (21.4 m^2/ha) compared with 25, 32 and 40 trees for the medium density thin, high density thin and untreated control, respectively (Table 2). In California, Fettig *et al*. (2010) found significant correlations between the percentage of pines killed by bark beetles and basal area (m^2/ha), number of trees, and stand density index (a measure of the density of a stand of trees based on dbh of tree of average basal area and number of trees per unit area; Reineke, 1933). The number of trees best predicted the amount of pine mortality attributed to bark beetles ($r^2 = 0.76$). Interestingly, no significant correlations were found between measures of stand density and the percentage of *A. concolor* killed by *S. ventralis* in their study (Fettig *et al*., 2010), which is in agreement with the findings of the present study.

Recent research on the impacts of thinning and thinning-and-burning treatments for fuels reduction and forest restoration in ponderosa pine and mixed-conifer stands have generally reported low bark beetle-caused tree mortality (Busse *et al*., 2009; Six & Skov, 2009; Fettig *et al*., 2010; Fettig & McKelvey, 2010) and reductions in fuel loads sufficient to increase fire resiliency (Schwilk *et al*., 2009). Fuel reduction treatments typically include thinning from below, retention of large diameter trees and tree species preferences (Agee & Skinner, 2005). The residual stand densities in our low density treatment are similar to those used in fuel reduction projects in similar stands, and should provide a significant reduction in fire hazard at the same time as reducing stand susceptibility to bark beetle infestation.

It should be emphasized that the amount of bark beetle-caused tree mortality reported in the present study is lower than expected, particularly in the high density thin and untreated control. A more substantial test of the resiliency of these treatments and resulting stand structures and compositions to bark beetle infestations will occur if bark beetle 'pressure' increases in the future. Our hope is to maintain this scientific infrastructure; to continue to monitor these plots on an annual basis for any changes in these effects over time, specifically in reference to the pine component; and to assess changes in individual tree growth and vigour associated with thinning treatments.

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