

Forest thinning and subsequent bark beetle-caused mortality in Northeastern California[☆]

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ABSTRACT

The Warner Mountains of northeastern California on the Modoc National Forest experienced a high incidence of tree mortality (2001–2007) that was associated with drought and bark beetle (Coleoptera: Curculionidae, Scolytinae) attack. Various silvicultural thinning treatments were implemented prior to this period of tree mortality to reduce stand density and increase residual tree growth and vigor. Our study: (1) compared bark beetle-caused conifer mortality in forested areas thinned from 1985 to 1998 to similar, non-thinned areas and (2) identified site, stand and individual tree characteristics associated with conifer mortality. We sampled ponderosa pine (*Pinus ponderosa* var *ponderosa* Dougl. ex Laws.) and Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) trees in pre-commercially thinned and non-thinned plantations and ponderosa pine and white fir (*Abies concolor* var *lowiana* Gordon) in mixed conifer forests that were commercially thinned, salvage-thinned, and non-thinned. Clusters of five plots (1/50th ha) and four transects (20.1 × 100.6 m) were sampled to estimate stand, site and tree mortality characteristics. A total of 20 pre-commercially thinned and 13 non-thinned plantation plot clusters as well as 20 commercially thinned, 20 salvage-thinned and 20 non-thinned mixed conifer plot clusters were established. Plantation and mixed conifer data were analyzed separately. In ponderosa pine plantations, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) caused greater density of mortality (trees ha⁻¹ killed) in non-thinned (median 16.1 trees ha⁻¹) compared to the pre-commercially thinned (1.2 trees ha⁻¹) stands. Percent mortality (trees ha⁻¹ killed/trees ha⁻¹ host available) was less in the pre-commercially thinned (median 0.5%) compared to the non-thinned (5.0%) plantation stands. In mixed conifer areas, fir engraver beetles (*Scolytus ventralis* LeConte) (FEN) caused greater density of white fir mortality in non-thinned (least square mean 44.5 trees ha⁻¹) compared to the commercially thinned (23.8 trees ha⁻¹) and salvage-thinned stands (16.4 trees ha⁻¹). Percent mortality did not differ between commercially thinned (least square mean 12.6%), salvage-thinned (11.0%), and non-thinned (13.1%) mixed conifer stands. Thus, FEN-caused mortality occurred in direct proportion to the density of available white fir. In plantations, density of MPB-caused mortality was associated with treatment and tree density of all species. In mixed conifer areas, density of FEN-caused mortality had a positive association with white fir density and a curvilinear association with elevation.

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1. Introduction

In Western North America, bark beetles (Coleoptera: Curculionidae, Scolytinae) are native forest insects whose endemic populations create canopy gaps for new growth by colonizing and killing older, diseased or declining trees (Cole and McGregor, 1988;

Lundquist and Negron, 2000). Bark beetles play a crucial role in forest nutrient cycling and promote biodiversity by providing forage for avian and other species (Furniss and Carolin, 1977; Martin et al., 2006). At outbreak population levels, beetles can cause extensive tree mortality altering forest structure, reducing fiber productive capacity, and diminishing stand aesthetics (Cole and McGregor, 1988; Fiddler et al., 1989; Cochran and Barrett, 1998). Increases in surface fuel loadings also follow bark beetle-caused mortality (Jenkins et al., 2008; Klutsch et al., 2009).

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) and fir engraver (*Scolytus ventralis* LeConte) (FEN) are economically important species whose outbreaks have led to extensive

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mortality in ponderosa pine (*Pinus ponderosa* var *ponderosa* Dougl. ex Laws.) and white fir (*Abies concolor* var *lowiana* Gordon) forests. For example, MPBs caused mortality of 870,000 trees from 1999 to 2003 in California and FENs contributed to the death of over 1.2 million trees in the forests of northern California from 1977 to 1978 (Ferrell, 1986; USDA, 2004).

Land managers and researchers have sought ways to reduce tree mortality caused by bark beetles since the early 1900s when direct control techniques to eliminate pre-flight bark beetle brood were extensively tested (Miller and Keen, 1960). While many methods of direct control are effective in causing brood mortality, application on a landscape-scale is ineffective or impractical for outbreak mitigation (Miller and Keen, 1960; Amman and Baker, 1972; Sartwell and Stevens, 1975). However, silvicultural treatments that manipulate stand density have been shown effective in reducing bark beetle-caused mortality in multiple forest types (Fettig et al., 2007).

Thinning is the reduction of stand density to reallocate growing space and increase vigor in residual trees (Oliver and Larson, 1990). Trees with low vigor can have greater risk of bark beetle attack and subsequent mortality after being attacked (Sartwell, 1971; Larsson et al., 1983). Thinning ponderosa pine can reduce competition leading to immediate decreases in water stress that can last from 8 to 16 years and contribute to increases in phloem thickness, net photosynthetic rates, and annual or periodic basal area increment growth rates (Kolb et al., 1998; Zausen et al., 2005). In true fir stands, thinning can increase residual tree vigor by 60% within two years of treatment while increasing diameter growth and net volume production (Oliver, 1988). Therefore, thinning may reduce bark beetle-caused mortality by alleviating inter-tree competition for scarce resources and increasing residual tree vigor.

Thinning can immediately influence stand microclimate while increases in tree vigor can have a multi-year lag period as trees respond to increased growing space (McGregor et al., 1987; Bartos and Amman, 1989; Amman and Logan, 1998). Benefits of thinning on bark beetle-caused tree mortality can be observed prior this lag period; thus, microclimate may be a mechanism by which thinning can reduce tree mortality (Hall and Davies, 1968; Amman and Logan, 1998). Microclimate variables that may influence MPB behavior or reproductive success after thinning include air temperature, solar radiation exposure, wind speed, and pheromone plume stability (Schmid et al., 1995; Amman and Logan, 1998; Thistle et al., 2004).

Evaluations of thinning in various forest types support this treatment as a means to reduce bark beetle-caused mortality. Thinning studies in ponderosa pine forests consistently report that thinning reduced the density of bark beetle-caused mortality (trees ha⁻¹ killed) or, where different thinning intensities were tested, areas with lower density had less percent mortality (trees ha⁻¹ killed/trees ha⁻¹ host available) compared to areas with higher density (Cole and McGregor, 1988; Fiddler et al., 1989; Schmid et al., 1994). Other studies, while not testing thinning practices directly, lend support to the thinning hypothesis by illustrating positive linear relationships found between ponderosa pine density and the density of MPB-caused mortality (Cole and McGregor, 1988; Fiddler et al., 1989; Oliver and Uzoh, 1997; Amman and Logan, 1998; Negron and Popp, 2004). Few studies have evaluated thinning efficacy in true fir forests. Cochran (1998) reported high levels of FEN-caused mortality in thinned and non-thinned true fir forests during drought conditions. In ponderosa pine/white fir and other mixed-species forests the efficacy of thinning has not been tested in experimental studies to-date (Fettig et al., 2007).

Our study was conducted in the Warner Mountains of northeastern California after a period of below average precipitation coincided with a high occurrence of bark beetle-caused tree mortality from 2001 to 2007 (CFPC, 2001–2007). The goal of this

research was to determine if thinning treatments are a viable tool to reduce bark beetle-caused mortality in mixed-species ponderosa pine/white fir stands and ponderosa/Jeffrey pine plantations during drought conditions. Our objectives were to: (1) compare the density and percent of bark beetle-caused tree mortality that occurred from 2001 to 2007 in thinned and non-thinned areas and (2) identify site, forest or individual tree characteristics associated with differing densities of bark beetle-caused mortality.

2. Methods

2.1. Study area

Our study area was the western slope of the Warner Mountains, Modoc National Forest, in northeastern California (Fig. 1). The Warner Mountains are an isolated range with a Mediterranean climate where most of the 38–76 cm of average annual precipitation falls as snow between November and April (PRISM 1961–1990; NRCS, 2010). Forests are primarily located on north-facing slopes that have deep molisol and alfisol soils (Peace, 1965; Vasek, 1978).

The study area was between 1620 and 2230 m and contained primarily ponderosa and Jeffrey pines (*Pinus jeffreyi* Grev. and Balf.) plantations and mixed ponderosa pine and white fir forests. Other tree species in the study area included western juniper (*Juniperus occidentalis* Hook.), incense cedar (*Calocedrus decurrens* Torrey), quaking aspen (*Populus tremuloides* Michx.), and western white pine (*Pinus monticola* Dougl. ex D. Don). Ecological plant association habitats (Smith, 1994) included ponderosa-white fir/serviceberry-oregongrape (*P. ponderosa*-*A. concolor*/*Amelanchier alnifolia* Nutt. ex M. Roem.-*Mahonia aquifolium* Pursh Nutt.), yellow pine-white fir/serviceberry-oregongrape (*P. ponderosa* and *P. jeffreyi*-*A. concolor*/*A. alnifolia*-*M. aquifolium*), and ponderosa-white fir/spreading snowberry (*P. ponderosa*-*A. concolor*/*Symphoricarpos mollis* Nutt.).

2.2. Silvicultural treatments surveyed

Forest management practices assessed included pre-commercial, commercial, and insect salvage thinning. Forest areas that were pre-commercially thinned (hereafter referred to as plantations) were planted at 1.2 m × 1.2 m spacing with ponderosa and Jeffrey pine seedlings as pure or mixed-species in the late 1930s and early 1940s after a stand-replacing fire in 1929 (Oliver and Uzoh, 1997). Plantations were pre-commercially thinned in the early 1990s to an average of 6.1 × 6.1 (range 4.3 × 4.3–7.0 × 7.0) m spacing and 274 (247–408) trees ha⁻¹. Areas that were commercially thinned or salvage-thinned (hereafter referred to as mixed conifer) were naturally regenerated stands of mixed-species dominated by ponderosa pine or white fir. Commercial thinning treatments took place at an average of 12 (7–13) years before the onset of tree mortality in 2001 with a mean residual basal area (BA) target of 37 (31–49) m² ha⁻¹. Salvage-thinning treatments occurred on average 5 (3–8) years prior to 2001 and combined salvage harvesting of bark beetle-killed trees with live-tree thinning to reduce BA to 25 (18–39) m² ha⁻¹.

Historical disturbances in the mixed conifer forests included grazing since the late 1800s, fire suppression since around 1910 and harvesting (primarily of pines) since the early 1900s. These disturbances, as well as MPB and western pine beetle (*Dendroctonus brevicomis* LeConte)-caused ponderosa pine mortality, likely contributed to an increase in the number and proportion of white fir trees in forested areas and grass-dominated meadows (Eaton, 1941; Vale, 1977).

Stands thinned from 1985 to 1998 were identified using the Forest Service Activity Tracking System (FACTS) geospatial database (Modoc National Forest), research of stand record cards, and field

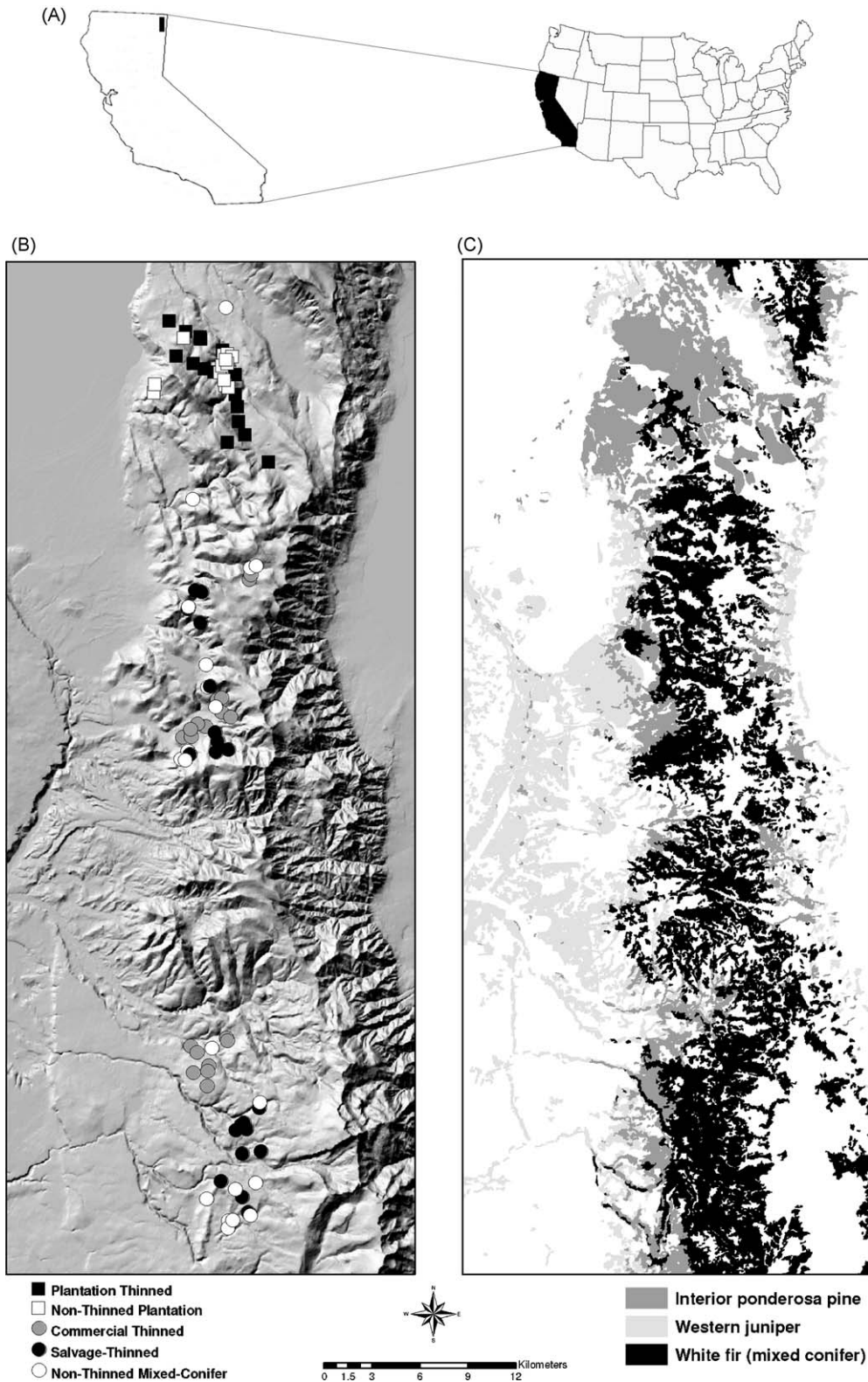


Fig. 1. (A) Geographic location of the Warner Mountain study area in northeastern California. (B) Warner Mountain topography and plot location by treatment, and (C) primary forest cover type distribution in the Warner Mountains. Topographic data were obtained from the USGS NED layer available online through ESRI ArcGIS information servers and forest cover type data were obtained from USDA Forest Service, Modoc National Forest.

visits. Field visits ensured areas did not experience confounding management activity or disturbance event (i.e. wildfire, prescribed fire application, subsequent management entries, etc.) following thinning. A total of 27 plantations, 10 commercially thinned, and 27

salvage-thinned mixed conifer stands met our treatment and time-since-treatment criteria and averaged 33 (11–112), 45 (6–162), and 30 (8–89) ha in area, respectively. As only 10 commercially thinned stands were available and field surveys indicated heterogeneous

forest structure and composition, we established multiple experimental units in stands and adjusted for repeated measurements. Non-thinned areas were located near (within 1.6 km) thinned stands to promote similar stand composition and bark beetle populations. A total of 13 non-thinned plantation and 20 non-thinned mixed conifer areas met our spatial proximity criteria.

2.3. Experimental design and sampling

Our experimental unit was a cluster of five plots and four transects (hereafter referred to as plot clusters) that were established to survey stands. Data collection occurred between May and August during 2006 and 2007. We surveyed a random selection of plantation stands with 20 pre-commercially thinned and 13 non-thinned plot clusters and mixed conifer stands with 20 plot clusters each in commercially thinned, salvage-thinned, and non-thinned stands. All stands had a plot cluster per stand except for the commercially thinned stands in which 20 plot clusters were located within 10 stands.

Plot clusters consisted of five fixed area (1/50th ha) plots to sample stand conditions and four transects (20.1 m × 100.6 m) to sample tree mortality. Plot clusters were randomly located in stands and oriented as a square with plots at each corner, one plot outside the square, and transects between the plots. Plot clusters were re-arranged to fit within narrow stands where needed but sampled area remained constant. Large commercially thinned stands were delineated into 6 ha segments to allocate multiple plot clusters per stand. The initial plot cluster was randomly located in a segment and additional clusters were located by randomly selecting the segment with the furthest distance (minimum 250 m) from the initial segment to promote independence. In non-thinned areas, a random driving distance, azimuth, and walk-in distance were assigned to locate the first plot as non-thinned areas were not previously delineated.

In plots we recorded spatial coordinates, elevation, percent slope, and aspect. Species, live/dead status, diameter at 1.4 m (DBH), and crown dominance class were recorded for all trees ≥ 2.5 cm DBH. Status, diameter, species, crown dominance class, and mortality agent were recorded for dead trees ≥ 10.2 cm DBH in transects. Mortality agent was designated as a bark beetle species by assessing inner-bark gallery patterns or recorded as agent other than bark beetles in the absence of galleries (Goheen and Willhite, 2006). Dead trees that exhibited needle retention, at least 25% fine branch retention, no sapwood or heartwood decay, and tight, intact bark were considered recent (≤ 5 years) mortality (Keen, 1929; Thomas, 1979).

2.4. Data analysis

Data from plantation and mixed conifer plot clusters were analyzed separately. Stand parameters (species composition, trees ha⁻¹, basal area, stand density index, quadratic mean diameter, diameter classes, and crown dominance classes) from each plot were reconstructed to 2001/2002 values by including all recent tree mortality and averaged to stand-level values. Stand density index (SDI) was calculated by the individual tree summation method and equations described in Reineke (1933). Only recent tree mortality data were analyzed as it was not possible to determine if time of death for older mortality was pre- or post-thinning. Thus, the reconstructed plot data describe stand characteristics in 2001/2002 prior to the period of tree mortality surveyed (2001–2007) in transects.

Forest and site characteristics were tested to ensure comparability between treatments with Student's *t*-tests of slope, elevation, and relative species composition variables. Similarly, plot density variables were tested between treatments to ensure thinned areas had reduced density compared to the non-thinned areas.

Table 1

Mean site and plot characteristics in Warner Mountain, CA pine plantations. Note: Means are unadjusted and were reconstructed from 2006 to 2007 plot data to 2001 to 2002 values when bark beetle-caused mortality began.

Variable	Pre-commercially thinned Mean ± SEM	Non-thinned Mean ± SEM
<i>Site conditions</i>		
Elevation (m)	1779 ± 14a	1707 ± 13b
Slope (%)	14.6 ± 1.6a	25.7 ± 2.1b
<i>Diameter</i>		
All species QMD ^A (cm)	37.3 ± 0.8a	33.5 ± 1.3b
Ponderosa pine QMD (cm)	37.3 ± 0.8a	34.5 ± 1.8a
Jeffrey pine QMD (cm)	36.6 ± 1.0a	31.5 ± 2.3b
<i>Density of all species</i>		
Density (trees ha ^{-1B})	271.8 ± 19.0a	503.4 ± 59.1b
Basal area (m ² ha ⁻¹)	29.6 ± 2.3a	39.0 ± 2.7b
SDI ^C	201.4 ± 15.1a	278.1 ± 20.8b
<i>Density by species</i>		
Ponderosa pine density (trees ha ⁻¹)	152.0 ± 32.6a	336.1 ± 66.2b
Ponderosa pine basal area (m ² ha ⁻¹)	17.4 ± 3.8a	28.1 ± 4.5a
Ponderosa pine SDI	116.9 ± 25.5a	196.4 ± 31.8a
Jeffrey pine density (trees ha ⁻¹)	104.5 ± 25.2a	121.6 ± 58.8a
Jeffrey pine basal area (m ² ha ⁻¹)	11.0 ± 2.8a	9.1 ± 4.2a
Jeffrey pine SDI	74.9 ± 18.9a	65.7 ± 30.6a
<i>Species composition</i>		
Proportion Jeffrey pine	0.43 ± .10a	0.20 ± .09a
Proportion ponderosa pine	0.49 ± .10a	0.69 ± .09a

Different letters denote significant difference in sampled variable between thinned and non-thinned plantation plots with Student's *t*-test at *p* < 0.05.

^A Quadratic Mean Diameter (QMD) calculated only from plots containing species indicated in variable name.

^B trees ha⁻¹ refers to the density of trees ≥ 2.5 cm DBH.

^C Stand Density Index (SDI) was calculated by summing individual tree SDI values derived from Reineke (1933) equations as described in Long and Daniel (1990).

The density of conifer mortality (trees ha⁻¹ > 10.2 cm killed from 2001 to 2007) and percent mortality (trees ha⁻¹ > 10.2 cm killed from 2001 to 2007/trees ha⁻¹ > 10.2 cm of host available in 2001/2002) variables were averaged from transects and plots then analyzed at the stand-level. Using percent and density of mortality as response variables, we tested for treatment effects between thinned and non-thinned plots for the primary bark beetle mortality agent in each study area. Only plots with a host component available for the primary bark beetle to colonize were retained. Analysis of covariance (ANCOVA) modeling was conducted with the density of mortality as the response with treatment and potential predictors not confounded with treatment including: elevation, slope, and relative species composition (trees ha⁻¹ of given species/trees ha⁻¹ of all species). For plantation data, the robust regression procedure was utilized to down-weight the influence of four outliers. Treatment differences were assessed with treatment covariate effects tests that utilize chi-square (χ^2) statistics (SAS Institute Inc., 2004). For mixed conifer data, a random effect model was used to adjust for repeated measurements. Random effects included plot clusters imbedded within stands while fixed effects included treatment and significant covariates. Treatment differences were tested with Tukey adjusted *p*-values calculated from least significant difference mean comparisons.

Robust and random effects models (as above) were used to identify stand and site characteristics associated with the density of conifer mortality in plantation and mixed conifer stands. The treatment covariate was retained in all models to represent our experimental design. Potential predictors included all variables in Tables 1 and 3. Stepwise regression procedures were not utilized due to the collinearity among predictor variables. Rather, the most significant predictor variable in effects tests was included

in an initial model. Residuals from the initial model were then plotted against all the other potential predictors to identify additional variables to incorporate. Variables with significant effects tests were retained in a best-fit model. The FEN-caused density of mortality response in the best-fit mixed-effect model was transformed (natural logarithm +1) to meet homogeneous error variance assumptions. A random effect model for plantations was also created in this manner to compare parameter estimates to the Robust model and for spatial analysis. Random effects included stand and fixed effects included treatment and any significant predictors.

Spatial autocorrelation among plots was assessed to verify plot independence. Variables from best-fit models were adjusted for spatial autocorrelations using the Mixed procedure in SAS (SAS Institute Inc., 2004). Then, spatially adjusted models were tested for differences against non-adjusted models with $-2 \log$ likelihood ratio statistics that have approximate chi-square distributions (Littell et al., 1996). For plantations, spatial analysis was limited to non-outlier data to meet model assumptions.

Individual tree diameter classes were assessed in the plantation and mixed conifer areas for association with tree mortality. The relative diameter class distribution of mortality from 2001 to 2007 was compared to respective 2001/2002 reconstructed diameter class distribution of live host trees. For each diameter class, we calculated the relative proportion of mortality (trees ha⁻¹ killed in each class/trees ha⁻¹ of all trees killed) and host available (trees ha⁻¹ live trees in each class/trees ha⁻¹ of all live trees) for each plot cluster. We then calculated the difference of these relative proportions with paired-plot Wilcoxon's signed rank tests (Hollander and Wolfe, 1973). Thus, for each treatment we tested each individual diameter class with the null hypothesis: no difference in the relative proportion of bark beetle-caused mortality and available host within each diameter class.

3. Results

3.1. Plantations

Plantations were sampled with data collected from 2887 trees. Percent slope and elevation differed in non-thinned and thinned stands (Table 1) but analysis indicated no association of slope or elevation with the density of conifer mortality. Proportion of ponderosa or Jeffrey pine species compositions did not differ between thinned and non-thinned plots (Table 1). Thinned plantation stands had less density and basal area of all species than non-thinned stands (Table 1 and Fig. 2A). The MPB caused the majority of density and percent mortality in thinned and non-thinned plantations (Table 2).

Thinned stands had reduced MPB-caused density of and percent mortality compared to non-thinned stands. Thinning treatment was a significant predictor in robust regression models with MPB-caused density of mortality and percent mortality as responses ($\chi^2 = 112.5, p < 0.001$ and $\chi^2 = 18.1, p < 0.001$, respectively). No other potential predictor variables were significant in these models. As robust regression models do not assess least square mean differences, median mortality values are described in Table 2 for thinned and non-thinned plantations.

Stand and site characteristics were assessed for association with MPB-caused density of mortality in robust regression models. Variables describing stand density calculated from all species influenced the density of MPB-caused mortality and other potential predictors were non-significant. The best-fit model had thinning treatment as a significant covariate ($\chi^2 = 21.5, p < 0.001$) and there was a positive, linear relationship (0.02 coefficient estimate) with trees ha⁻¹ of all species ($\chi^2 = 11.9, p < 0.001$) (Fig. 3). All species SDI and basal area explained less residual error than trees ha⁻¹ but had

Table 2

Median conifer mortality values for pine plantations surveyed in the Warner Mountains, CA 2006–2007.

Mortality agent	Pre-commercially thinned Median (plots)	Non-thinned Median (plots)
<i>Density of mortality^a</i>		
All bark beetle	2.5 (20)	22.2 (13)
Other than bark beetles	0.0 (20)	1.2 (13)
Mountain pine beetle	1.2 (15)	16.1 (13)
Western pine beetle	0.0 (15)	2.5 (13)
Jeffrey pine beetle	0.0 (11)	0.0 (13)
<i>Percent mortality^b</i>		
All bark beetle	0.7 (20)	4.0 (13)
Other than bark beetles	0.0 (20)	0.3 (13)
Mountain pine beetle	0.5 (15)	5.0 (13)
Western pine beetle	0.0 (15)	0.5 (13)
Jeffrey pine beetle	0.0 (11)	0.0 (6)

^a Density of mortality is the trees ha⁻¹ >10.2 cm killed from 2001 to 2007 while

^b percent mortality is the trees ha⁻¹ >10.2 cm killed from 2001 to 2007/trees ha⁻¹ >10.2 cm of host available in 2001/2002. Only plots containing host trees were used in individual bark beetle-caused mortality calculations.

similar, positive linear relationships with the response ($\chi^2 = 5.23, p = 0.022$ and $\chi^2 = 3.46, p = 0.063$). Ponderosa pine density variables (SDI, basal area, and trees ha⁻¹) did not have a detectable influence on the density of MPB-caused mortality ($\chi^2 = 0.70, p = 0.402, \chi^2 = 1.03, p = 0.310$, and $\chi^2 = 0.35, p = 0.553$, respectively).

Similarly, variables describing stand density calculated from all species influenced the density of MPB-caused mortality in a mixed model that excluded the four outlier data points. Treatment was a significant covariate ($F_{1,21} = 12.3, p < 0.002$) and the density of MPB-caused mortality had a positive relationship (0.02 coefficient estimate) with trees ha⁻¹ of all species ($F_{1,21} = 12.6, p = 0.002$). No evidence of spatial autocorrelation was found when comparing this mixed model to a model adjusted for spatial autocorrelation ($\chi^2 = 0.00, p = 0.999$).

3.2. Mixed conifer areas

Mixed conifer areas were sampled with data collected from 13,722 trees. Percent slope and elevation did not differ between commercially thinned and non-thinned stands or between salvage-thinned and non-thinned stands (Table 3). Proportion of ponderosa pine and white fir species compositions did not differ between commercially thinned and non-thinned stands. However, greater white fir relative density was found between salvage-thinned and non-thinned stands (Table 3). Thus, analysis of mortality between salvage-thinned and non-thinned stands occurred in models that adjusted for white fir composition. The non-thinned mixed conifer areas had significantly greater density and basal area of all species compared to the commercially thinned stands and the salvage-thinned stands (Table 3; see Fig. 2B). The FEN caused the majority of density and percent mortality in mixed conifer stands (Table 4).

Thinned mixed conifer stands had a reduced density of FEN-caused mortality compared to non-thinned stands. Modeling FEN-caused density of mortality indicated treatment was a significant predictor ($F_{2,47} = 7.52, p = 0.002$) after adjusting for elevation ($F_{1,47} = 6.09, p = 0.017$), elevation² ($F_{1,47} = 6.55, p = 0.014$), and relative white fir species composition ($F_{1,47} = 14.6, p < 0.001$). Other potential predictors were not significant. FEN-caused density of mortality differed between commercially thinned (23.8 ± 5.7 trees ha⁻¹) and non-thinned (44.5 ± 5.4 trees ha⁻¹) stands ($p = 0.026$) and for salvage-thinned (16.4 ± 5.4 trees ha⁻¹) compared to non-thinned stands ($p = 0.002$). No difference was detected between commercially thinned and salvage-thinned stands ($p = 0.662$).

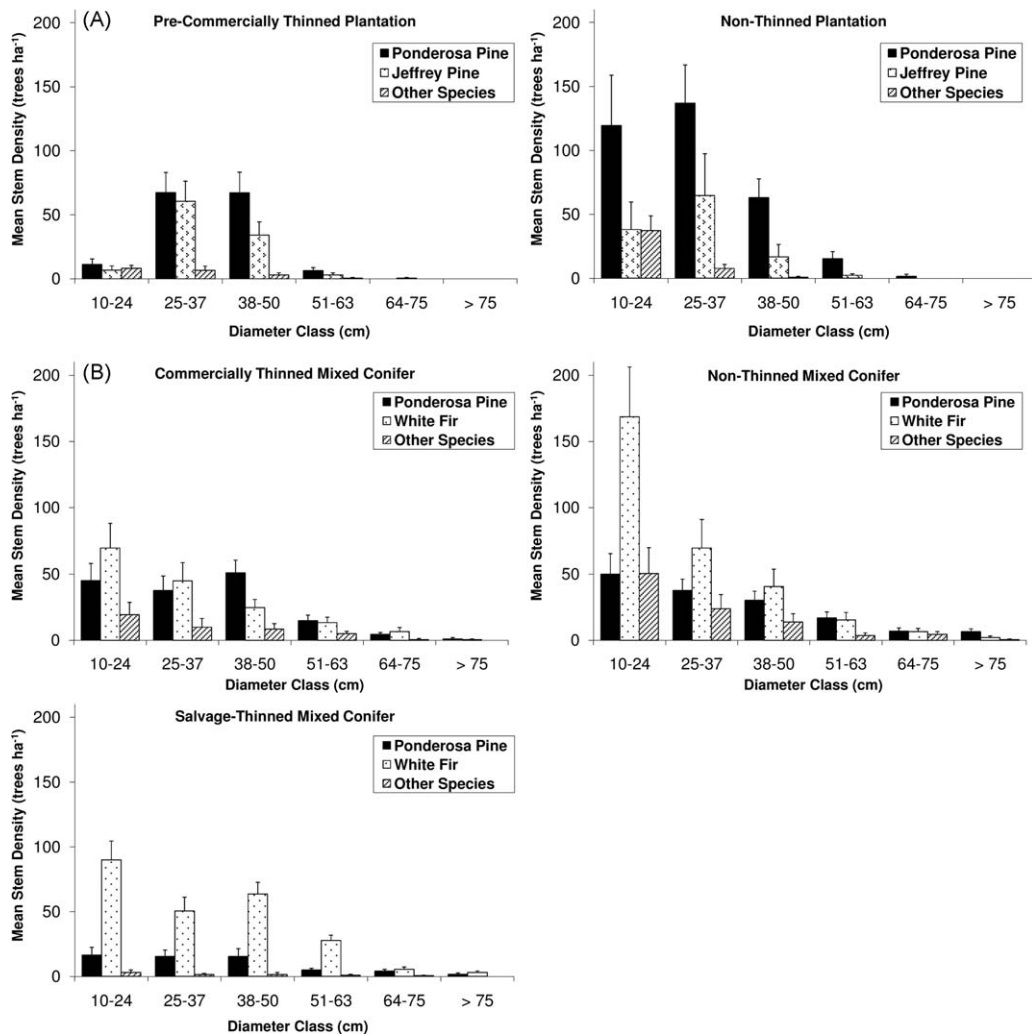


Fig. 2. Mean stem density (trees ha⁻¹ reconstructed to 2001/2002) ± standard error by diameter class and species for (A) plantation and (B) mixed conifer stands.

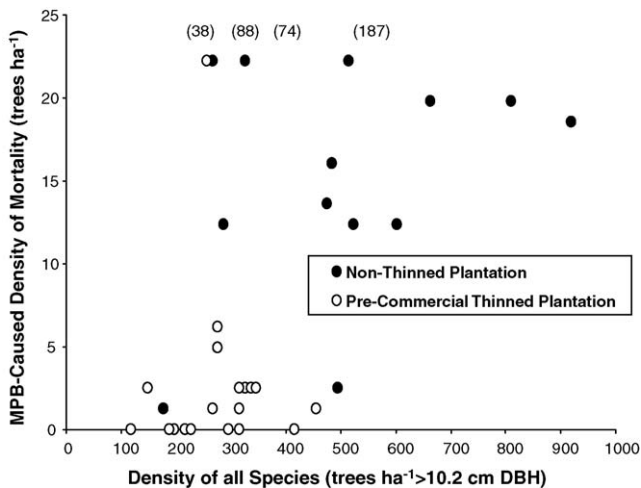


Fig. 3. Scatter plot of density of mountain pine beetle (MPB)-caused ponderosa pine mortality from 2001 to 2007 by density of all species reconstructed to 2001/2002 values. Four outlier plots are truncated to $y=22$ while parenthesis signify actual y values for plot scale and to depict plots down-weighted for robust regression modeling.

Thinned and non-thinned mixed conifer stands had no difference in percent FEN-caused mortality. Models incorporated only the treatment covariate as no potential predictor variables were significant. Thinning treatment was not significant ($F_{2,50} = 0.18$, $p = 0.834$), indicating no difference of least square means for percent mortality between commercially thinned ($12.6 \pm 0.03\%$), non-thinned ($13.1 \pm 0.03\%$), or salvage-thinned ($11.0 \pm 0.03\%$) stands.

Stand and site characteristics were assessed for association with FEN-caused density of mortality in mixed regression models. Variables describing white fir host density, white fir QMD, and elevation were associated with density of FEN-caused mortality and all other variables in Table 3 were non-significant. Initial introduction of the treatment covariate indicated a significant effects test at $\alpha = 0.10$ ($F_{2,50} = 2.95$, $p = 0.062$) but when white fir density (trees ha⁻¹ ≥ 10.2 cm) was added to the model the treatment effect was non-significant ($F_{2,49} = 1.32$, $p = 0.276$). Similarly, white fir QMD had a significant, positive association in initial models but was not significant in models that included white fir density. White fir density (trees ha⁻¹) had greater descriptive power ($F_{1,49} = 21.9$, $p < 0.001$) than treatment or any other potential predictor of FEN-caused density of mortality.

The initial model indicated white fir density had a linear, positive association with the density of FEN-caused mortality (Fig. 4A). Interaction tests indicated no difference in the slope of this relationship between treatments ($F_{2,47} = 0.90$, $p = 0.412$), which is consistent with the lack of a treatment effect on percent mortal-

Table 3
Mean site and plot characteristics for Warner Mountain, CA mixed conifer areas. Note: Means are unadjusted and were reconstructed from 2006 to 2007 plot data to 2001 to 2002 values when bark beetle-caused mortality began.

Variable	Commercially thinned Mean ± SEM	Non-thinned Mean ± SEM	Salvage-thinned Mean ± SEM
<i>Site conditions</i>			
Elevation (m)	1834 ± 34a	1894 ± 32ax	1964 ± 16x
Slope (%)	16.8 ± 2.0a	17.7 ± 2.3ax	16.1 ± 1.5x
<i>Diameter</i>			
All species QMD ^A (cm)	38.9 ± 1.3a	35.6 ± 1.0ax	39.6 ± 0.2x
Ponderosa pine QMD (cm)	40.6 ± 2.8a	45.0 ± 2.8ax	41.1 ± 2.8x
Jeffrey pine QMD (cm)	40.4 ± 2.3a	41.7 ± 6.6bx	33.8 ± 8.6x
White fir QMD (cm)	36.1 ± 2.0a	29.5 ± 2.0bx	37.3 ± 1.8y
<i>Density of all species</i>			
Density (trees ha ^{-1B})	356.3 ± 29.9a	546.6 ± 51.2bx	305.4 ± 24.0y
Basal area (m ² ha ⁻¹)	37.2 ± 1.5a	52.3 ± 4.5bx	35.5 ± 2.0y
SDI ^C	245.9 ± 11.0a	346.4 ± 28.1bx	229.4 ± 12.2y
<i>Density by species</i>			
Ponderosa pine density (trees ha ⁻¹)	153.7 ± 30.9a	147.8 ± 30.9ax	58.1 ± 13.1y
Ponderosa pine basal area (m ² ha ⁻¹)	17.8 ± 3.0a	20.4 ± 3.8ax	7.7 ± 1.7y
Ponderosa pine SDI	116.2 ± 20.1a	124.9 ± 22.7ax	47.6 ± 10.5y
Jeffrey pine density (trees ha ⁻¹)	9.4 ± 7.4a	58.3 ± 32.9ax	4.0 ± 2.2x
Jeffrey pine basal area (m ² ha ⁻¹)	0.8 ± 0.6a	5.5 ± 2.8ax	0.4 ± 0.3x
Jeffrey pine SDI	5.3 ± 3.7a	36.4 ± 18.8ax	2.7 ± 1.6x
White fir density (trees ha ⁻¹)	159.6 ± 36.3a	302.5 ± 67.5ax	239.9 ± 25.0x
White fir basal area (m ² ha ⁻¹)	15.2 ± 3.1a	23.7 ± 6.1ax	26.9 ± 2.3x
White fir SDI	101.7 ± 20.8a	166.3 ± 40.0ax	176.0 ± 14.1x
<i>Species composition</i>			
Proportion ponderosa pine	0.45 ± .08a	0.30 ± .06ax	0.19 ± .04x
Proportion Jeffrey pine	0.02 ± .01a	0.12 ± .06ax	0.01 ± .01x
Proportion white fir	0.44 ± .09a	0.50 ± .09ax	0.78 ± .05y

Different letters denote significant difference in sampled variable between commercially thinned and non-thinned plots (ab) and salvage-thinned and non-thinned plots (xy) with Student's *t*-test at $p < 0.05$. Commercially and salvage-thinned plots were not compared.

^A Quadratic Mean Diameter (QMD) calculated only from plots containing species indicated in variable names.

^B trees ha⁻¹ refers to the density of trees ≥ 2.5 cm DBH.

^C Stand Density Index (SDI) was calculated by summing individual tree SDI values derived from Reineke (1933) equations as described in Long and Daniel (1990).

ity. White fir basal area and white fir SDI, while explaining less residual error than white fir trees ha⁻¹, were also significant predictors ($F_{1,49} = 5.81$, $p = 0.020$ and $F_{1,49} = 9.58$, $p = 0.003$) and had positive relationships with the density of FEN-caused mortality. SDI and basal area of all species were not significant predictors ($F_{1,49} = 1.88$, $p = 0.176$ and $F_{1,49} = 0.39$, $p = 0.536$). The best-fit model of FEN-caused white fir mortality indicated a positive, linear relationship with white fir trees ha⁻¹ ($F_{1,47} = 31.6$, $p < 0.001$) and a curvilinear relationship with elevation as represented by elevation and elevation² in the model ($F_{1,47} = 13.8$, $p < 0.001$ and $F_{1,47} = 14.6$, $p < 0.001$, respectively) (Fig. 4). The thinning treatment covariate

was not significant ($F_{2,47} = 0.18$, $p = 0.834$) in the best-fit model. A mixed-effect model that adjusted for spatial autocorrelation was not significantly different than the best-fit model ($\chi^2 = 0.37$, $p = 0.829$).

3.3. Individual tree characteristics associated with mortality

The diameter distributions of MPB but not FEN-caused mortality differed from the diameter distributions of live host trees in respective plantations and mixed conifer stands (Fig. 5). Significantly greater amounts of MPB-caused tree mortality was concentrated

Table 4
Median conifer mortality values for mixed conifer areas surveyed in the Warner Mountains, CA 2006–2007.

Mortality agent	Commercially thinned Median (plots)	Non-thinned Median (plots)	Salvage-thinned Median (plots)
<i>Density of mortality^a</i>			
All bark beetle	14.3 (20)	40.8 (20)	27.9 (20)
Other than bark beetles	1.2 (20)	4.4 (20)	3.2 (20)
Fir engraver ^c	9.9 (17)	37.1 (16)	21.0 (20)
Mountain pine beetle	2.5 (16)	5.7 (16)	1.2 (19)
Western pine beetle	0.0 (16)	0.0 (16)	0.0 (19)
Jeffrey pine beetle	0.7 (4)	8.2 (4)	1.2 (3)
<i>Percent mortality^b</i>			
All bark beetle	4.8 (20)	8.2 (20)	9.0 (20)
Other than bark beetles	0.4 (20)	0.9 (20)	0.8 (20)
Fir engraver ^c	7.0 (17)	13.1 (16)	8.4 (20)
Mountain pine beetle	1.2 (16)	4.4 (16)	1.2 (19)
Western pine beetle	0.0 (16)	0.0 (16)	0.0 (19)
Jeffrey pine beetle	3.1 (4)	4.8 (4)	6.3 (3)

^a Density of mortality is the trees ha⁻¹ >10.2 cm killed from 2001 to 2007 while ^bpercent mortality is the trees ha⁻¹ >10.2 cm killed from 2001 to 2007/trees ha⁻¹ >10.2 cm of host available in 2001/2002. Only plots containing host trees were used in individual bark beetle-caused mortality calculations. ^cFir engraver-caused white fir mortality values are unadjusted.

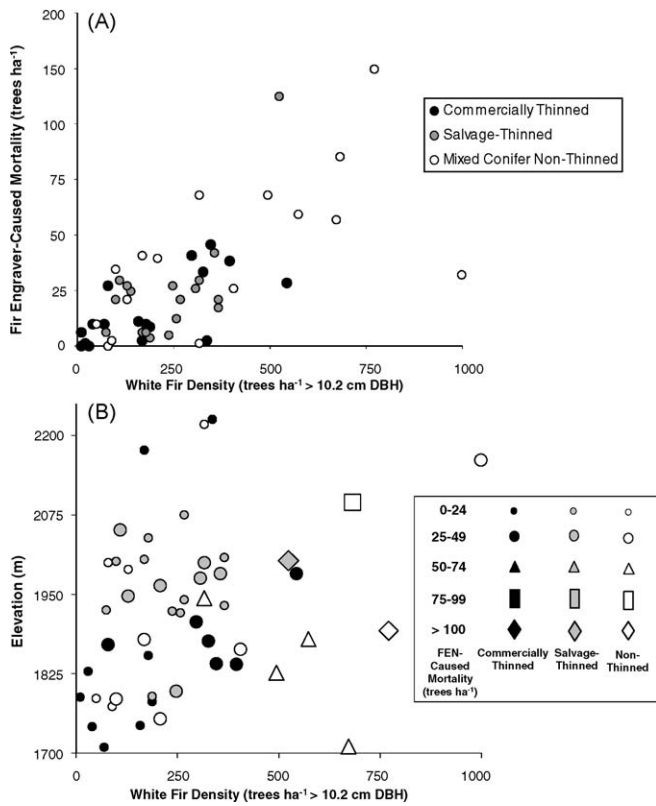


Fig. 4. (A) Scatter plot of initial linear model with best predictor: density of fir engraver (FEN)-caused white fir mortality from 2001 to 2007 by white fir density reconstructed to 2001/2002 values. (B) 3-Dimensional scatter plot of best-fit model with varied density of FEN-caused mortality by elevation and white fir density.

in the 10–24 cm ponderosa pine diameter class in non-thinned mixed conifer stands and in the 25–37 cm diameter class in pre-commercially thinned plantation stands compared to available host in those diameter classes (Fig. 5). Significantly less MPB-caused mortality was also found in salvage-thinned mixed conifer, pre-commercially thinned plantation, and non-thinned plantation stands for the 38–50 cm ponderosa pine diameter class; as well as in the commercially thinned mixed conifer, non-thinned mixed conifer, pre-commercially thinned plantation, and non-thinned plantation stands for the 51–63 cm diameter class. No significant differences were found in any plantation or mixed conifer stands for the 64–75 cm and >76 cm ponderosa pine diameter classes (data not shown). Significantly less FEN-caused tree mortality only occurred in mixed conifer commercially thinned <25 cm and salvage-thinned 51–64 cm diameter classes.

4. Discussion

4.1. Mortality in plantation areas

The MPB caused significantly less density of mortality and percent mortality in the pre-commercially thinned compared to the non-thinned stands suggesting that thinning reduced the density of mortality and changed the ratio of mortality to host abundance. Changes in biological factors, such as residual tree vigor and stand microclimate, likely interacted with the host reduction to reduce MPB-caused ponderosa pine mortality in thinned areas.

Density of mortality was reduced in thinned areas and correlated with measures of stand density including trees per area, basal area, and SDI. These density variables all had a positive, linear relationship with the density of mortality similar to findings in previous studies that evaluated MPB-caused mortality in ponderosa pine

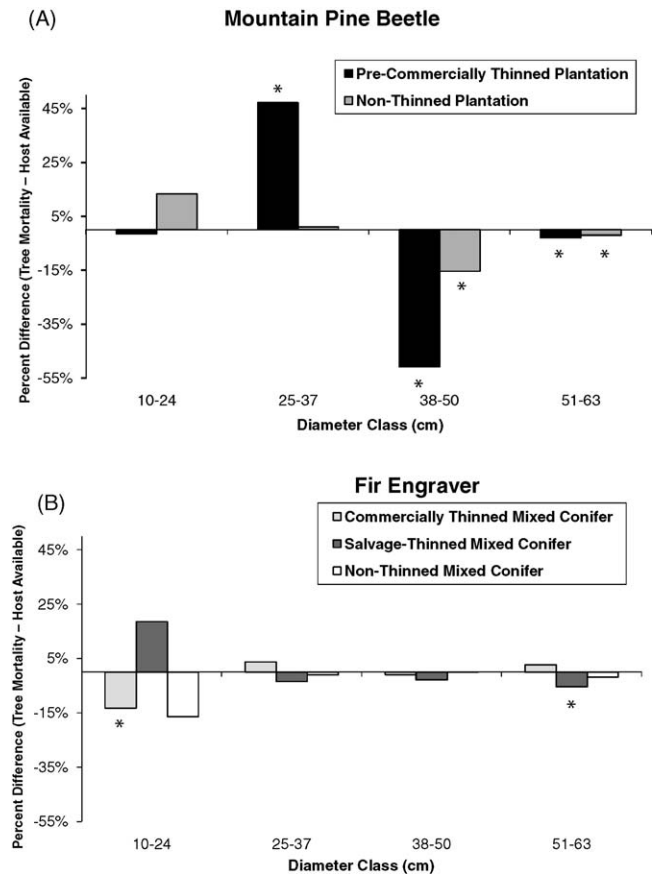


Fig. 5. Median difference (relative percent mortality from 2001 to 2007—relative percent of host available in 2001/2002) within each diameter class by beetle species. *Denotes paired-plot significant differences indicated within each treatment and diameter class at alpha = .05. Diameter classes >64 cm are not shown and had no median difference between mortality and diameter distribution.

forests (Fiddler et al., 1989; Oliver and Uzoh, 1997; Negron and Popp, 2004; Schmid and Mata, 2005; Fettig et al., 2007). Interestingly, the outlier points that prompted the robust regression analysis occurred in plots that had mid-range stand density values from 300 to 600 trees ha⁻¹. Outlier plots included one thinned and three non-thinned plantation stands that were all located in close proximity (within 0.3–0.8 km). This suggests that proximity to MPB population epicenters or other spatially dependant environmental factors were correlated with MPB-caused mortality in outlier stands. Our models could not simultaneously adjust for outliers and spatial covariance; thus, the assumption of plot independence may not have been met in models that included the outlier data. However, analysis with and without the outlier plots yielded similar results of a treatment effect and a linear, positive relationship, with similar slope estimates, between stand density of all species and MPB-caused density of ponderosa pine mortality. No evidence of spatial autocorrelation of MPB-caused density of mortality was found in the non-outlier data.

4.2. Mortality in mixed conifer areas

The FEN beetle caused the majority of mortality in all mixed conifer treatments, and density of FEN-caused mortality was less in all thinned compared to the non-thinned areas. However, percent mortality did not differ as 11–13% FEN-caused mortality occurred in both thinned and non-thinned areas. Thus, the thinned areas had reduced numbers of dead trees compared to non-thinned areas and tree mortality occurred in direct proportion to the abundance of

white fir available. This suggests that the treatments did not influence vigor or microclimate sufficiently to facilitate a difference in the relationship between white fir mortality and host abundance described by percent mortality. Cochran (1998) found similar results in southern Oregon after high levels of mortality occurred in white fir/grand fir thinned to varied densities. After a drought period from 1991 to 1995, high ranges of FEN-caused percent mortality occurred in each residual stocking level (7–27% at 112 SDI, 14–46% at 168, 24–63% at 224, and 19–79% at 280). Cochran (1998) did not conduct a replicated test but noted that the density of and percent mortality appeared to have a positive relationship with stand density. In this study we found a similar positive relationship with the density of mortality but percent mortality appeared constant throughout the range of stand densities surveyed. This difference may be due to FEN host complexes as Cochran's (1998) study plots contained white and grand fir, both suitable hosts for FEN, while our plots consisted of white fir and non-host species.

Our models indicated density of FEN-caused mortality had a positive association with white fir density and a curvilinear relationship with elevation. The association with elevation is likely a proxy for water availability but other factors such as temperature, varied growing seasons, acclimation of trees to water availability and trends of pure white fir stands at higher elevations may have been important. The association of FEN-caused mortality with white fir density is consistent with the similar percent mortality values found between all treatments. These findings are similar to other studies that have described positive relationships correlating density or basal area of bark beetle-caused true fir mortality and host abundance (Moore et al., 1978; Ferrell et al., 1993, 1994; McMillin et al., 2003). Interestingly, we found no evidence that the density of FEN-caused mortality varied by spatial location among plots that ranged along the latitudinal extent of the Warner Mountains (Fig. 1). This suggests that our assumption of plot independence, especially as non-thinned plots were located adjacent to thinned plots, was valid. This also suggests that other spatially distributed factors such as proximity to FEN population epicenters, soil profiles or microclimate did not have a detectable influence on the density of FEN-caused mortality surveyed.

Four biological factors can potentially explain the mixed conifer results after making assumptions about FEN population pressures. These include: (1) vigor of residual host trees, (2) changes in microclimate, (3) beetle success in finding host trees, and (4) the attraction of beetles to host kairomones. Assuming constant bark beetle population pressure, forest density or competition would be a limiting variable in FEN-caused density of mortality in factors 1 and 2.

In our study, overall competition, through the proxy of thinned and non-thinned treatments and stand density variables, did not appear to have a strong association with the FEN-caused density of mortality. Rather, the density of FEN-caused mortality varied with the density of white fir that may have been independent of overall (combined host and non-host) stand density. These density variables are partially collinear but there are multiple non-thinned data points that have similar FEN-caused density of mortality values as thinned plots at constant white fir density (see Fig. 4A). Thus, the beetle success or host kairomone factors are likely more important than host vigor or microclimate in explaining our results. Assuming constant FEN population pressure, beetle success ratios could be affected by the ratio of host to non-host trees as dispersing beetles experience greater mortality with longer search times in a host-limited environment. While possible, this factor seems unlikely to produce such a clear, consistent success rate (gauged by percent mortality) for FEN beetles across all the stand densities, species compositions, and spatial locations surveyed.

Therefore, we hypothesize that the attraction to host semiochemicals was the biological regulation of the consistent relationship between FEN-caused mortality and white fir host available as FEN population pressure was proportionally directed towards stands with varied host abundance. FEN does not utilize an aggregation pheromone to initiate mass attacks on host trees; rather, this species responds to kairomones released from potential host trees (Macias-Samano et al., 1998). The density and occurrence of FEN attacks can occur in residual trees located near thinned or logged areas where slash was created before beetle flight, indicating the FEN beetle response to host volatiles (Ferrell, 1973; Livingston et al., 1979). Under water stress grand fir trees, which are genetically similar and hybridize often with white fir trees, are unable to illicit any kind of defensive response to external stimuli such as mechanical wounding (Lewinsohn et al., 1993). Thus, as the white fir were likely stressed from the recent drought period, possibly to the point where defense against attacking bark beetles was negligible, the numbers of adult FEN attracted into these mixed conifer areas was just enough to cause an average of 11–13% mortality in white fir trees regardless of thinning.

4.3. Individual tree characteristics associated with mortality

In plantation stands, relative MPB-caused mortality was not proportional to the diameter distribution of available host trees and was skewed away from larger diameter classes (>38 cm DBH). These results are consistent with those found by Olsen et al. (1996) in the Black Hills, South Dakota where MPB preferentially caused mortality in microcosm areas with relatively lower quadratic mean diameter values in the Black Hills, South Dakota. However, Negron and Popp (2004) noted in the Colorado Front Range the proportion of MPB-killed trees to live trees increased with increasing diameter classes. Similarly, Negron et al. (2008) reported in the Black Hills, South Dakota, the greatest percentage of MPB-caused mortality occurred in the 37.5–52.5 cm classes. Differences found in these studies relative to our study may be due to differing site qualities, regionally adapted MPB populations, different bark beetle population pressures, genetic heterogeneity of ponderosa pine hosts, different stand conditions (age, understory prevalence, canopy structure, etc.), varying stand microclimates, proximity to beetle population epicenters or a combination of these and other unknown factors (Sturgeon and Mitton, 1986; Amman and Logan, 1998; Bentz et al., 2001).

FEN did not cause white fir mortality in any consistent pattern that varied from the diameter distribution of available host trees in the mixed conifer areas. This is consistent with previous studies where FEN-caused mortality was not skewed towards certain diameter classes (Livingston et al., 1979; Ferrell, 1986).

5. Conclusions

Our findings support thinning ponderosa pine plantations to reduce MPB-caused mortality during periods of below average precipitation where bark beetles have the potential to kill many trees. These results agree with previous research that show thinning is an effective tool to reduce the density of MPB-caused mortality in pure ponderosa pine stands (Sartwell and Stevens, 1975; Fiddler et al., 1989; Schmid and Mata, 2005; Fettig et al. 2007). All recorded percent MPB-caused mortality values $\geq 10\%$ in this study occurred in plots that exceeded 300 trees ha⁻¹ or 200 SDI. Similar results from other studies in northern California and Washington reported minimum stand susceptibility thresholds of 186 and 250 SDI, respectively (Oliver and Uzoh, 1997; Cochran and Barrett, 1998). The magnitude by which both the percent and density of mortality was reduced, and with the close proximity of

non-thinned and thinned areas, suggests that using residual tree spacing targets can be very effective in protecting thinned plantations even during periods of drought.

Our findings varied in mixed conifer areas as the density of, but not percent, FEN-caused mortality was reduced in thinned areas. These results do not support the use of thinning to reduce percent mortality or the relative number of residual white fir trees susceptible to FEN-caused mortality during times of drought. Conversely, this study does support the efficacy of thinning to reduce the density of mortality or absolute number of beetle-killed trees in mixed conifer stands exposed to drought conditions. The density of residual white fir host and elevation (likely a proxy for water availability) were important factors associated with white fir mortality in our study. These findings indicate thinning effectiveness in reducing fir mortality was directly proportional to the amount of post-treatment density white fir retained. Thus, our findings support discriminating against residual fir and retaining a greater pine component, similar to historic compositions (Vale, 1977), during thinning treatments to reduce the density of FEN-caused mortality even during periods of drought.

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