Long-term efficacy of diameter-limit cutting to reduce mountain pine beetle-caused tree mortality in a lodgepole pine forest

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ABSTRACT

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is the most significant mortality agent in pine forests of western North America. Silvicultural treatments that reduce the number of susceptible host trees, alter age and size class distributions, and diversify species composition are considered viable, long-term options for reducing stand susceptibility to mountain pine beetle-caused tree mortality. Short-term efficacy of thinning treatments has been evaluated, but long-term efficacy has not. We evaluated mountain pine beetle-caused lodgepole pine mortality in 2008, ~28 years after diameter-limit cutting from above that removed the largest diameter lodgepole pines in a Wyoming, USA forest. Following extensive recent mountain pine beetle activity, the partially-cut stands had significantly less mountain pine beetle-caused tree mortality compared to untreated reference stands. These results are similar to observations five years post-treatment, albeit using different reference stands because the original controls were lost to timber harvest. The original management objective was reduced mountain pine beetle-caused tree mortality, and this objective was achieved, lasting for up to 28 years. Despite the reduced mortality among partially-cut stands, however, untreated and treated stands had similar densities of residual live mature lodgepole pine and those in untreated stands had larger average diameters.

Key words: lodgepole pine, *Dendroctonus ponderosae*, silviculture, vegetation management, thinning

RÉSUMÉ

Le dendroctone du pin ponderosa, *Dendroctonus ponderosae* Hopkins, représente le plus important agent de mortalité des pinèdes de l'ouest de l'Amérique du Nord. Les traitements sylvicoles qui réduisent le nombre d'arbres susceptibles d'être atteints, qui modifient la distribution selon l'âge et les classes de diamètres et qui permettent la diversification de la composition des espèces, s'avèrent être des mesures viables à long terme pour réduire la susceptibilité des peuplements aux ravages causés par le dendroctone du pin. L'efficacité à court terme des traitements d'éclaircie a été évaluée, mais pas celle à long terme. Nous avons évalué la mortalité provoquée chez le pin ponderosa par le dendroctone du pin en 2008, environ 28 ans après une coupe à diamètre limite qui a retiré les pins de fort diamètre dans une forêt du Wyoming aux États-Unis. À la suite d'une recrudescence marquée de l'activité récente du dendroctone, les peuplements ayant été partiellement coupés ont affiché une mortalité associée au dendroctone significativement plus faible par rapport aux peuplements témoins. Ces résultats sont similaires aux observations faites cinq ans après traitement, malgré l'utilisation de peuplements de référence différents compte tenu que les témoins originaux avaient été récoltés. L'objectif original d'aménagement était de réduire la mortalité provoquée par le dendroctone du pin et il a été atteint, et ce au cours des 28 années écoulées. Toutefois, malgré cette mortalité réduite parmi les peuplements ayant été partiellement coupés, les peuplements non traités et traités affichaient des densités semblables de pins ponderosa résiduels à maturité et ceux dans les peuplements non traités avaient les plus forts diamètres.

Mots clés : pin ponderosa, *Dendroctonus ponderosae*, sylviculture, contrôle de la végétation, éclaircie

Introduction

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae), a bark beetle species native to western North America, is commonly recognized as the most important mortality agent in coniferous forests of this region. Due to substantial economic losses caused by this insect, land managers have continually sought effective management strategies for minimizing tree mortality at the stand and landscape levels (Hopkins 1905, Fettig *et al.* 2014, Gillette *et al.* 2014). Early efforts to directly control beetle populations, using tactics such as applying insecticides and diesel fuel or burning infested trees, were eventually deemed unsuccessful or of moderate or temporary benefit (Craighead *et al.* 1931, Amman and Baker 1972). More recently, semiochemicals and insecticides have been shown to be effective at reducing mountain pine beetle-caused tree mortality for individual trees or groups of trees (Gillette *et al.* 2014), although semiochemical efficacy is greatly reduced when populations reach epidemic levels (Progar *et al.* 2014). Rather than directly targeting the insect population, indirect control focuses on reducing the probability and severity of future outbreaks by modifying stand characteristics conducive to beetle population success. Indirect control is thought to provide longer lasting efficacy against losses to bark beetles compared to direct control methods (Amman and Logan 1998, Fettig *et al.* 2014).

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Beginning in the early 1970s, multiple research efforts have identified stand-level factors such as species composition, stand density, tree age, basal area (BA), and average tree diameter at breast height (dbh) as factors related to mountain pine beetle outbreaks (Amman *et al.* 1977, Shore and Safranyik 1992, Bentz *et al.* 1993, Negrón and Popp 2004, Whitehead *et al.* 2004). Due to the link between stand conditions and outbreak probability and severity, vegetation management techniques were advocated to reduce beetle-caused mortality (Whitehead and Russo 2005, Fettig *et al.* 2007). For example, it is known that the largest diameter lodgepole pines (*Pinus contorta* Dougl. ex Loud.), trees typically with the thickest phloem, are attacked during the onset of a mountain pine beetle outbreak (Eveden and Gibson 1940, Cole and Amman 1969, Preisler and Mitchell 1993). Removal of large-diameter trees, often referred to as diameter-limit cutting or thinning from above (Helms 1998), was therefore recommended to reduce mountain pine beetle-caused tree losses in lodgepole pine stands (Cahill 1978, McGregor *et al.* 1987). Thinning has additional benefits including enhanced vigor among residual trees (Mitchell *et al.* 1983, Waring and Pitman 1985), and stand microclimate alterations that adversely influence bark beetle attack, reproduction, and brood success, as well as disrupt movement of semiochemicals important to the mass attack process (Bartos and Amman 1989, Schmid *et al.* 1992, Thistle *et al.* 2004). Several studies have found evidence that a decrease in stand BA, tree density, and mean dbh through thinning can reduce losses to mountain pine beetle in lodgepole (Mitchell *et al.* 1983, McGregor *et al.* 1987, Amman *et al.* 1988, Whitehead and Russo 2005) and ponderosa pine (*P. ponderosa* Dougl. Ex Laws.) (McCambridge and Stevens 1982, Schmid and Mata 2005, Zhang *et al.* 2013) stands relative to unthinned stands. While these studies reported results after a relatively short period of time following treatment (<10 years), to our knowledge, the long-term efficacy of diameter-limit cutting and other thinning types is undocumented.

One study area used to test the efficacy of diameter-limit cutting to reduce losses to mountain pine beetle was the East Long Creek Demonstration Area, Shoshone National Forest, Wyoming, USA (Cole *et al.* 1983). This project area was treated between 1979 and 1981 and was used to test management options identified by Cole and Cahill (1976) and Cahill (1978) as potentially reducing future losses to mountain pine beetle. Three diameter-limit cutting treatments, thinned from above to remove large diameter trees, were applied to remove all lodgepole pine larger than 17.8 cm (hereafter referred to as 18-cm cut), 25.4 cm (hereafter referred to as 25-cm cut), and 30.5-cm cut (see Cole *et al.* 1983 for details). After the treatments were completed, the project area was affected by mountain pine beetle activity, and a subsequent 5-year post-treatment survey indicated that partially cut stands had significantly less beetle-caused pine mortality than untreated control stands (Amman *et al.* 1988). Beetle-caused mortality in treatments was 1.8% in the 18-cm, 2.4% in the 25-cm, and 7.4% in the 30.5-cm diameter-limit cuts, whereas untreated stands sustained 26.5% beetle-caused mortality.

Our goal was to evaluate the long-term efficacy (~28 years post-treatment) of diameter-limit cutting to reduce losses to mountain pine beetle using the study area initiated by Cole *et al.* (1983) and monitored by Amman *et al.* (1988) on the Shoshone National Forest. National Insect and Disease Detection Surveys (NIDDS) conducted by the US Forest Service indicated that mountain pine beetle was active in the study area between 2002 and 2009 (U.S. Department of Agriculture 2002–2009). After a reconnaissance in 2007 to verify that the study area was mostly intact, we resurveyed the area in 2008–2009 utilizing methods similar to the Amman *et al.* (1988) survey. Our main objective was to compare mountain pine beetle-caused tree mortality in treatments partially cut 28 years prior with tree mortality in untreated stands. We also report residual stand conditions, including regeneration, 22 years (i.e., 2002 pre-outbreak) and 28 years (i.e., 2008 post-outbreak) following the diameter-limit cuts, and provide a comparison with stand conditions five years post-treatment (data from Amman *et al.* 1988). We discuss the long-term influence of diameter-limit treatments on stand structure and composition, and subsequent mountain pine beetle-caused tree mortality.

Methods

Study area and plot measurements

The study area is located in the East Long Creek drainage, Shoshone National Forest, Wyoming (Fig. 1). It contains approximately 768 ha of mixed conifer and pure lodgepole pine stands, ranging in elevation from 2318 to 2684 m. The climate is cool and dry, and minimal summer moisture may be a limiting growth factor. Cover types vary with aspect and elevation but subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) is considered the climax species. Pre-treatment successional status of lodgepole pine varied across the study area, ranging from heavily stocked pole-sized lodgepole pine stands to late-successional stands with spruce (*Picea engelmannii* Parry ex Engelmann) and fir replacing lodgepole pine. Lodgepole pines in most stands were 150–200 years-old, although some stands were younger. Site index values range from 9.1–15.2 m in 50 years. Before treatments in 1979–1981, the total basal area ranged from 14.4–31.1 $m^2 ha^{-1}$ (see Cole *et al.* 1983 for more details).

The original treatments, conducted 1979–1981, included 29 stands treated with one of three diameter-limit cutting regimes that removed all lodgepole pine above 18 cm, 25 cm, or 30.5 cm (Cole *et al.* 1983). Note that the original diameter-limit cuts were focused only on lodgepole pine. Limber pine (*P. flexilis* James), a minor component throughout the treatment area, was not harvested, resulting in remnant pockets of large-diameter limber pines remaining within treated stands. Project constraints included protection of key resource values, removal of merchantable timber via commercial timber sale, and road development for general access and land management. Cutting prescriptions were applied for the primary purpose of removing the most susceptible host trees, but other criteria were consider for each stand "to fit the condition of the stand and its ecology to promote future development under natural conditions" (Cole *et al.* 1983). The 18-cm diameter-limit cuts were applied to late transitional stands converting to shade tolerant spruce and fir, two-aged lodgepole pine stands with few tolerant species present, and heavily-stocked pole-size lodgepole pine stands. The 25-cm diameter-limit cuts were applied to stands dominated by lodgepole pine but with sparse stocking and on more southerly or westerly aspects (Cole *et al.* 1983). The original study had a single

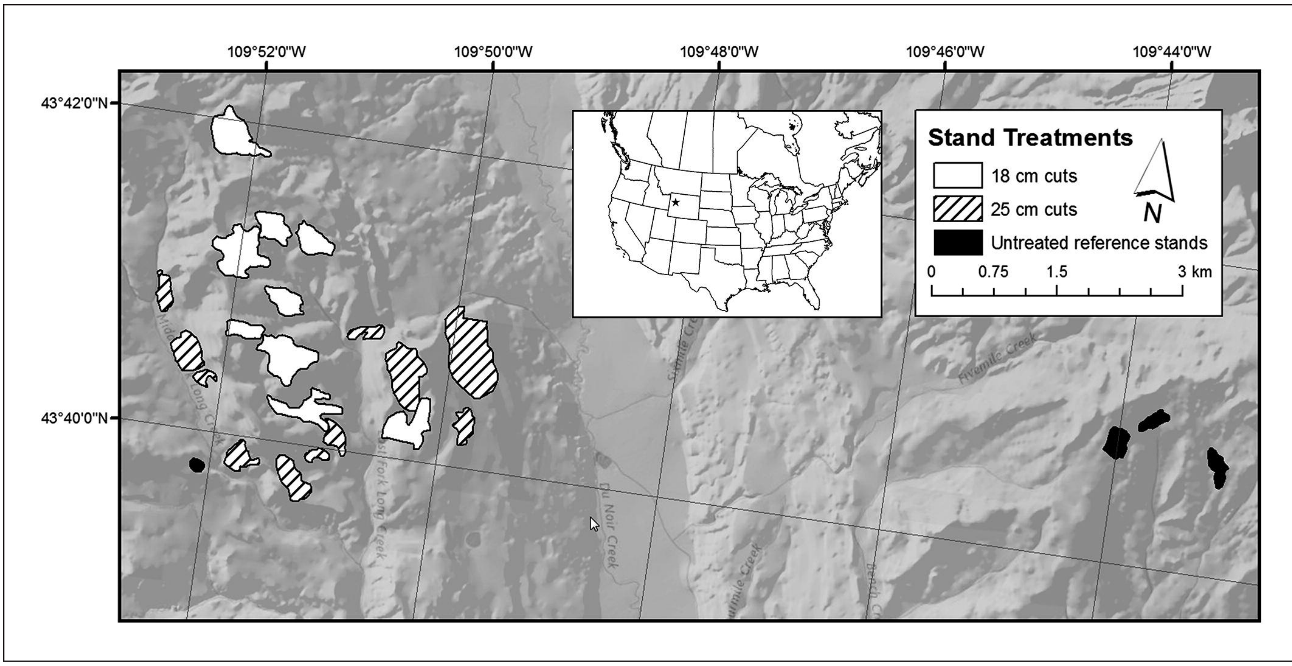


Fig. 1. Locations of diameter-limit cutting treatments and untreated reference stands surveyed in 2008–2009 on the Shoshone National Forest, Wyoming. Diameter-limit cuts were completed between 1979–1981 and the landscape experienced mountain pine beetle outbreaks in 1981–1985 and 2002–2009. Stand and cutting treatment boundaries were redrawn from the original silvicultural prescription maps. Two diameter-limit cutting treatments, thinned from above, were resurveyed including nine 18-cm and eleven 25-cm cutting units. Because the original untreated control stands were harvested after the surveys reported by Amman *et al.* (1988), four new reference stands were identified and surveyed.

control stand and Amman *et al.* (1988) added a second control stand; both of these were near the lower elevations of the study area in areas dominated by lodgepole pine. Like stands wherein the 25-cm diameter-limit cuts were applied, the control stands had relatively few shade-tolerant species present.

Some stands have been lost to fire or harvest since the Amman *et al.* (1988) surveys, including both of the original untreated stands, all 30.5-cm diameter-limit cutting units, and some of the 18- and 25-cm diameter-limit cutting units. We relocated and surveyed nine out of the original ten 18-cm diameter-limit cuts and eleven out of the original seventeen 25-cm diameter-limit cuts (Fig. 1). With the loss of the original untreated stands, we located and surveyed four replacement stands. Because most of the East Long Creek drainage has now been logged, we located only a single untreated stand to use as a control in the immediate vicinity of the partially cut units and near the locations of the original control stands. Three additional untreated stands were identified in a neighboring drainage of uncut lodgepole pine, about 8 km to the east (Fig. 1), ranging in elevation from 2713 to 2804 m. Criteria for selection of replacements included stands: 1) with no evidence of mechanical harvest; 2) dominated by mature lodgepole pine; and, 3) of similar elevation, aspect, and geology compared to the East Long Creek study area. To underscore that these replacement stands are different than the original controls, we hereafter call them "reference stands". Mountain pine beetle population pressure was very high in both areas as this was a landscape-scale event. Analysis of NIDDS data showed about 17 000 pines infested, from 2002–2008, within 3 km of the East Long Creek study area and about 25 000 pines infested within 3 km of the reference stands 8 km to the east.

We were unable to directly compare stand conditions through time using data from Cole *et al.* (1983), Amman *et al.* (1988), and the present study. Not only were the untreated stands different in the current study, but each study subsequent to Cole *et al.* (1983) sampled a different subset of the original diameter-limit cutting units. For example, Amman *et al.* (1988) only surveyed five out of the original ten 18-cm diameter-limit cuts and nine out of the original seventeen 25-cm diameter-limit cuts. Moreover, Cole *et al.* (1983) and Amman *et al.* (1988) reported pooled data by treatment, rather than by stand, and species-specific metrics were not always reported. Therefore, we were limited in ability to directly compare stand conditions from the current survey to those of the earlier surveys.

Maps and aerial photography with hand-drawn stand boundaries from the original 1979 silvicultural prescription on the Shoshone National Forest were obtained from Rocky Mountain Research Station historical records associated with the Cole *et al.* (1983) study. Spatial information was transferred into ArcMap (ESRI 2009), and new maps were created. Most of our surveys were conducted during 2008. The untreated reference stands, as well as a few additional plots within the diameter-limit treatments, were surveyed in early summer of 2009. To minimize bias due to timing of measurements, any 2009 attacked trees were considered to be uninfested in the analyses.

Our surveys were based on the sampling protocols established by Amman *et al.* (1988), which included a double sampling scheme. Variable radius plots (10 BA factor) were used to characterize stand conditions and structure, and 20.1 m-wide strip cruise plots were used for a more robust sampling of mountain pine beetle-caused tree mortality throughout each stand. The variable radius plots were spaced according to stand size at 60.4 m–100.7 m intervals and were located in a grid pattern. The number of plots per stand was proportional to stand size and ranged from five to 24[1]. Strip cruises were conducted in the zone between the variable radius plots, and the length of each strip extended from the first to last variable radius plot with respect to the continuous, linear survey lines (e.g., a row of four variable radius plots running east to west). Regeneration was measured at each variable radius plot centre using 1/750 ha fixed-radius plots to tally trees < 12.7 cm dbh by species and size class (0 cm = 0.0–2.4 cm; 5 cm = 2.5–7.4 cm; 10 cm = 7.5–12.6 cm). The dbh of all live trees > 12.7 cm were also measured and pines were categorized as live, mountain pine beetle-killed, or other mortality. In the strip cruise plots, only diameters of mountain pine beetle-killed trees were recorded. Note that this included only trees from the 2002–2008 outbreaks; trees infested during the early 1980s had fallen. Mountain pine beetle-killed trees were assigned a year of attack based on foliage color and needle retention (Wulder *et al.* 2006).

Stand conditions at the beginning of the recent outbreak (i.e., 2002) were estimated by recoding recently-killed trees (i.e., between 2002 and 2008) as live. By estimating conditions pre-outbreak, we were able to characterize changes in stand structure and composition due to the 2002–2008 outbreaks. Although reported data were limited in the earlier surveys, we compared mountain pine beetle impact on stand conditions during the recent outbreak with impact recorded after a 1981–1985 outbreak. Metrics of BA (all species), trees ha^{-1} (all species), and trees ha^{-1} (lodgepole pine only) in 1981 and 1985 were taken from Cole *et al.* (1983) and Amman *et al.* (1988). We also report residual conditions in the partially cut and untreated reference stands 28 years post-treatment, following extensive mountain pine beetle-caused tree mortality between 2002 and 2008.

Statistical analyses

Generalized linear mixed models (Littell *et al.* 2006, PROC GLIMMIX, SAS Institute, Inc., Cary, NC) were used to detect differences among the treated (i.e., 18- and 25-cm diameter-limit cuts) and untreated reference stands. Differences in residual stand conditions and regeneration among treatments and reference stands were analyzed using data from the variable radius plots. Data from the strip cruises were used to analyze differences in mountain pine beetle-caused tree mortality. Pairwise comparisons of the treatments were made using the Tukey-Kramer multiple comparison test. Tree mortality was expressed as proportions of trees and BA killed, analyzed separately for lodgepole and limber pines. To express tree mortality as a proportion for the strip cruise data, wherein only mountain pine beetle-infested pines were recorded, we used pine population data from the variable radius plots for the denominator (i.e., pre-outbreak pine density or BA). Residual stand conditions were expressed as trees and BA ha^{-1}. Ratios of generalized chi-square to degrees of freedom were used to check for overdispersion. Model residuals were assessed for normality using Q-Q plots. When the response variable was tree density or BA we specified a Poisson, log-normal or negative binomial error distribution (an *a posteriori* decision based on residuals and overdispersion) whereas a binomial error distribution was specified for proportional data. Denominator degrees of freedom were specified as Kenward-Roger type.

Some response variables included multiple zero observations (e.g., tree density of less common tree species such as limber pine which was absent on many plots), resulting in poor residual distributions. For these analyses, we instead used a zero-inflated Poisson regression model (PROC GENMOD, ZEROMODEL statement, SAS Institute, Inc., Cary, NC) with a multiple range test based on the Wald chi-square statistic. In a few analyses, zero-inflated Poisson regression models did not converge or were inappropriate because the data sets contained few zeroes. For these cases, we used the non-parametric Multi-Response Permutation Procedure (Euclidean distance) which included multiple distribution comparisons (Turner 2006). Results from generalized linear mixed models are reported with a *t*-statistic, results from zero-inflated Poisson regression models are reported with a chi-square statistic, and results from Multi-Response Permutation Procedures are reported with a standardized test statistic.

Results

Beetle-caused tree mortality between 2002 and 2008.

Mountain pine beetle activity in the study area began in 2002 and declined by 2009. Between 2002 and 2008, 22- and 28-years post-treatment, the proportion of beetle-killed lodgepole and limber pine in untreated reference stands was significantly greater than the proportion killed in either the 25-cm or 18-cm diameter-limit cuts (Fig. 2)[2]. The proportions of lodgepole and limber pine killed did not significantly differ among the two diameter-limit cutting treatments. Results were similar regarding proportions of basal area killed except that, for lodgepole pine, the reference and 18-cm diameter-limit cut stands were only marginally different ($p = 0.0596$).

Residual stand conditions in 2008

Twenty-eight years post-treatment (i.e., 2008), and following a severe mountain pine beetle outbreak, the density of live lodgepole pine (≥ 12.7 cm dbh) in untreated reference stands did not significantly differ from that in diameter-limit cut stands. BA of lodgepole pine in reference stands also did not differ from the 25-cm cuts but was significantly greater than that in the 18-cm cuts. Both density and BA of lodgepole pine was lower in the 18-cm cuts compared to 25-cm cuts (Fig. 3)[3]. The density of live limber pine, which was not harvested in the original treatments, was greater in the reference stands than either diameter-limit cutting treatments, while limber pine density did not differ between the two diameter-limit cuts (Fig. 3). However, live limber pine BA was less in the

[1]Stand conditions, including stand size and the number of plots per stand, are given in supplementary Table S1. All supplementary tables are available only from the electronic version of this paper.

[2]See supplementary Table S2 for statistical result of pairwise-comparisons.

[3]See supplementary Table S3 for statistical result of pairwise-comparisons.

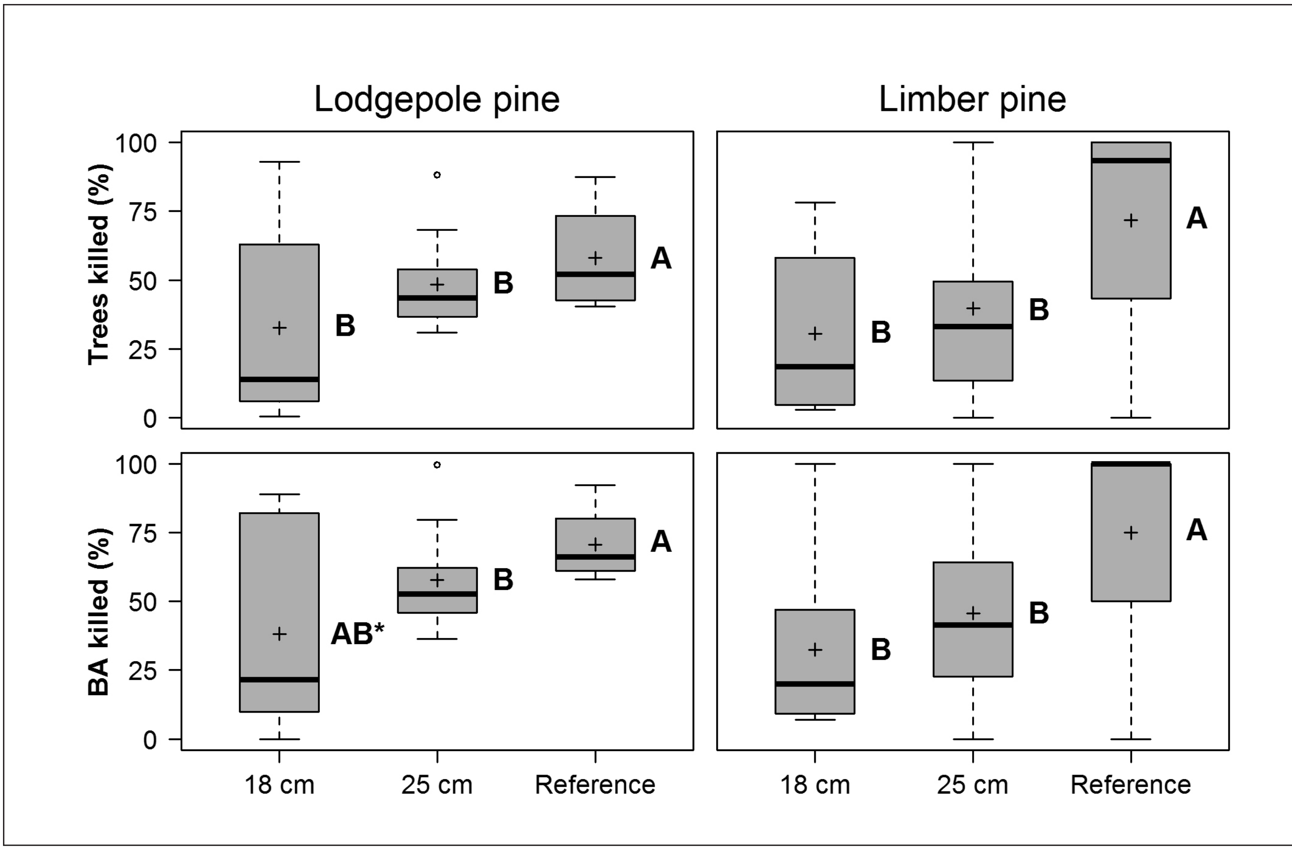


Fig. 2. Percent of lodgepole and limber pine killed by mountain pine beetle between 2002 and 2008 in 18- and 25-cm diameter-limit cutting treatments and untreated reference stands based on strip cruise plot data. Diameter-limit treatments occurred in 1979–1981. Treatments with the same letter within each panel were not significantly different using multiple range tests (α = 0.05). *Differences were marginally different (supplementary Table S2). Solid lines are the median, plusses the means, boxes the 25th and 75th percentiles, whiskers are 1.5 times the interquartile range, and circles are outliers.

25-cm cuts than in either the reference stands or 18-cm cuts. The density and BA of non-pine species [subalpine fir, Engelmann spruce, quaking aspen (*Populus tremuloides* Michx.), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco)] was less in the 25-cm cuts compared to the 18-cm cuts and reference stands (Fig. 3), reflecting pre-treatment stand conditions. Tree density and BA of non-pines in 18-cm cuts, however, was not different from that in reference stands (Fig. 3).

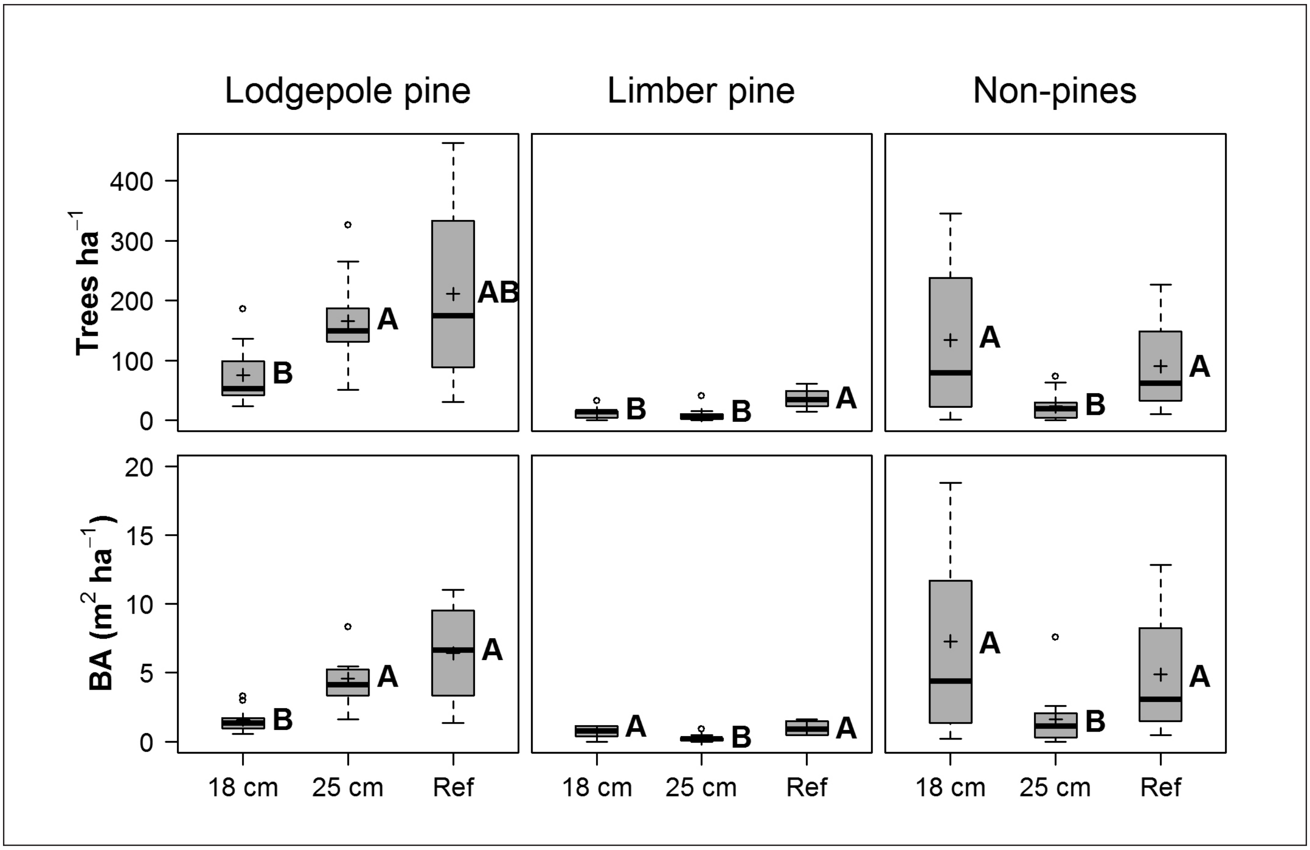
Regeneration in 2008

The density of lodgepole pines did not differ between the diameter-limit cutting treatments or between treated and untreated reference stands in any regeneration size class (i.e., 0 cm, 5 cm, 10 cm; Fig. 4)[4]. The reference stands had significantly more 0-cm size class limber pines than either cutting treatment and there were significantly more 5-cm size class limber pine in the 25-cm cuts compared to 18-cm cuts (Fig. 4). Otherwise, the densities of limber pine regeneration did not differ among treated and reference stands. There were no significant differences in the density of non-pine species between the diameter-limit cutting treatments or between treatments and reference stands in the 0-cm and 5-cm size classes. In the 10-cm size class, the 18-cm cuts had significantly more non-pine trees than the 25-cm cuts, but did not differ from the reference stands (Fig. 4).

Stand conditions five, 22 and 28 years post-treatment.

Cole *et al.* (1983) reported stand conditions in partially cut and untreated stands in 1981, following treatments, and Amman *et al.* (1988) reported conditions in 1985 after a mountain pine beetle outbreak between 1981 and 1985. We compared these reported values of mean residual BA (all species), trees ha^{-1} (all species), and lodgepole pine ha^{-1} to values from our resurveys that reflect conditions 22 years (i.e., 2002, pre-outbreak) and 28 years (i.e. 2008, post-outbreak) post-treatment. Because untreated reference stands in our resurveys were different, and different subsets of the original partially cut stands were surveyed, our comparison reports generic changes rather than stand-specific differences through time. Changes in stand conditions between five years post-treatment and 22 years post-treatment reflect recruitment and growth during that interval (Table 1). In the 18-cm cuts, total live tree density almost doubled, in large part due to increases in subalpine fir (data not shown). In the 25-cm cuts, however, the 31% increase in tree density was mostly due to an increase in lodgepole pine. On average, mean diameter of live lodgepole pine decreased between five and 22 years post-treatment in the diameter-limit cutting

[4]See supplementary Table S4 for statistical result of pairwise-comparisons.



.**Fig. 3.** Residual live stem density (top panels) and BA (bottom panels) of trees ≥ 12.7 cm dbh in 2008, 28 years after diameter-limit cutting treatments and after mountain pine beetle outbreaks in 1981–1985 and 2002–2008. Non-pines are subalpine fir, Engelmann spruce, quaking aspen and Douglas-fir. Treatments with the same letter within each panel were not different using a multiple range test ($\alpha = 0.05$) (supplementary Table S3). Solid lines are the median, plusses the means, boxes the 25th and 75th percentiles, whiskers are 1.5 times the interquartile range, and circles are outliers.

treatments, most likely due to ingrowth of advance regeneration and recruitment. The three-fold BA growth among untreated stands is likely because our reference stands were not the same as the control stands reported in Amman *et al.* (1988), although these stands almost certainly added some amount of BA since 1985. Therefore, untreated stand conditions are presented in Table 1 only for comparison to partially cut stands of the same year rather than stand development from 1985 to 2002.

In the 18-cm and 25-cm diameter-limit cuts, the percentage of lodgepole pine attacked and killed by mountain pine beetle between 2002–2008 (18-cm cuts: 32.6%; 25-cm cuts: 48.4%) was far greater than that observed between 1980–1985 (18-cm cuts: 1.8%; 25-cm cuts: 2.4%). Although untreated reference stands in 2002–2008 were not the same as the control surveyed in 1985, mountain pine beetle-caused tree mortality in untreated stands was also greater (1980–1985: 26.5%; 2002–2008: 58.0%). Mountain pine beetle-caused tree mortality after 2002 resulted in a 26%, 48%, and 60% reduction in lodgepole pine density in the 18-cm cuts, 25-cm cuts, and reference stands, respectively. Limber pine density decreased 45%, 44% and 79% in the 18-cm cuts, 25-cm cuts, and reference stands, respectively. Very few lodgepole and limber pine > 25 cm dbh survived the mountain pine beetle outbreak between 2002 and 2008, resulting in a reduction in mean dbh in all stands (Fig. 5). Moreover, the 18-cm cuts did not have *any* surviving lodgepole pine in diameter classes ≥ 30 cm compared to about 16 residual lodgepole pines ha^{-1} in reference stands in diameter classes ≥ 30 cm.

Discussion

Previous studies have demonstrated short-term (i.e., < 10 years) efficacy of thinning to reduce losses to mountain pine beetle in lodgepole pine (Mitchell *et al.* 1983, McGregor *et al.* 1987, Amman *et al.* 1988, Whitehead and Russo 2005). Our goal was to evaluate the long-term (i.e., > 25 years) efficacy of diameter-limit cuts from above, to 18-cm and 25-cm dbh, in reducing mountain pine beetle-caused tree mortality. We surveyed stands in the Shoshone National Forest that had been treated in 1979–1981 (Cole *et al.* 1983), and soon thereafter experienced mountain pine beetle-caused tree mortality (Amman *et al.* 1988). In 1985, five years post-treatment, treated stands had reduced tree mortality compared to untreated control stands (Amman *et al.* 1988). The area was again exposed to mountain pine beetle activity beginning 22 years post-treatment (i.e., 2002) and we resurveyed the stands in 2008 using replacement reference stands because the Amman *et al.* (1988) control stands were harvested after the 1985 surveys. Although the recent mountain pine beetle population was larger than that recorded by Amman *et al.* (1988), our results indicate that

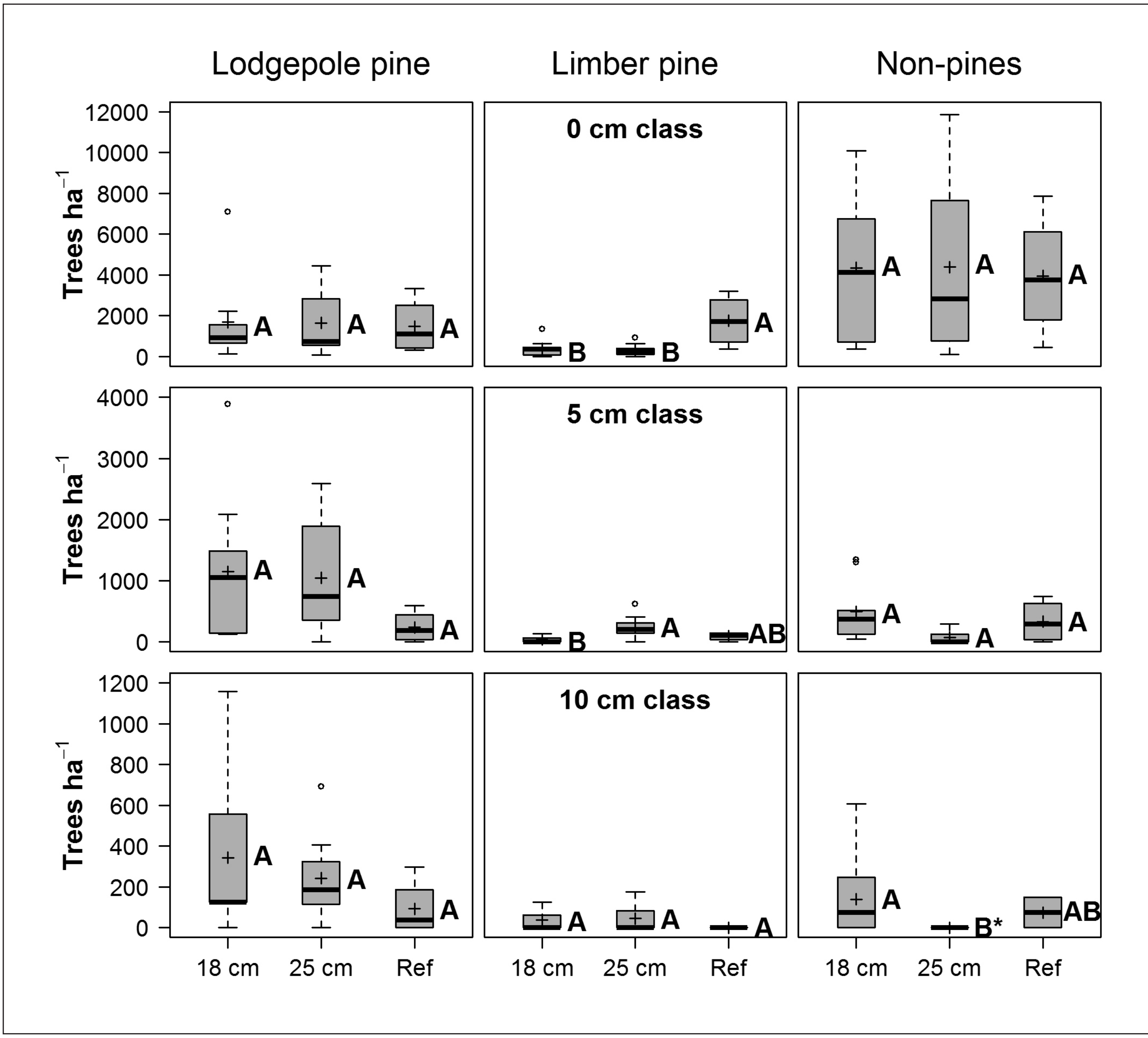


Fig. 4. Regeneration density in 0- (top panels), 5- (middle panels), and 10-cm (bottom panels) diameter classes for lodgepole pine, limber pine, and non-pines (subalpine fir, Engelmann spruce, quaking aspen, and Douglas-fir) in diameter-limit cutting treatments (18 cm and 25 cm) and untreated reference stands following mountain pine beetle outbreak in 2002–2008. Partial cutting treatments occurred in 1979–1981. Treatments with the same letter within each panel were not significantly different using multiple range tests (α = 0.05). *Tree density differences were marginally significant (supplementary Table S4). Solid lines are the median, plusses the means, boxes the 25th and 75th percentiles, whiskers are 1.5 times the interquartile range, and circles are outliers.

28 years post-treatment, the diameter-limit treatments continued to have significantly reduced mountain pine beetle-caused pine mortality compared to untreated reference stands.

A caveat regarding these results is that, because of harvesting following the 1985 surveys, our untreated reference stands were different than the untreated control stands used by Amman *et al.* (1988). It should be noted, however, that when the study was initiated by Cole *et al.* (1983), the East Long Creek study area was not a homogenous lodgepole pine forest but rather an area of forest dominated by mature lodgepole pine with varying stand densities and proportions of non-pine components. Moreover, assignment of treatments was not randomized as part of the demonstration project (Cole *et al.* 1983). The combined (i.e., 18-cm and 25-cm) diameter-limit prescriptions were applied to stand conditions ranging from sparsely-stocked lodgepole pine with few shade-tolerant species to heavily-stocked lodgepole pine to late transitional lodgepole pine with invasion by spruce and fir. In contrast, the original control plots used by Amman *et al.* (1988) were just outside the Demonstration Area boundary, near the lower elevational limits of the study area where lodgepole pine was relatively sparse with minimal stocking of shade-tolerant species. Our replacement reference stands were placed at a range of elevations, with stand conditions more representative of the range of conditions to which diameter-limit cuttings were applied. Moreover, all stands were subjected to very high levels of beetle population pressure during the 2002–2008 outbreaks.

Table 1. Stand conditions and mountain pine beetle-caused lodgepole pine mortality 28 years after diameter-limit cutting treatments (to 18-cm and 25-cm dbh, lodgepole pine only) in treated and untreated stands before and after beetle outbreaks ca. 1981–1985 and ca. 2002–2008, Shoshone National Forest, Wyoming.

	Treatment		
Stand character	**18-cm cuts**	**25-cm cuts**	**Untreated**
1981 to 1985 mountain pine beetle outbreak			
BA, 1981 (all species, $m^2\,ha^{-1}$)	6.4	8.5	18.8
Trees per ha, 1981 (all species)	209.8	224.3	452.5
Lodgepole pine killed (%)	1.8	2.4	26.5
BA, 1985 (all species, $m^2\,ha^{-1}$)	5.0	9.4	9.6
Trees per ha, 1985 (all species)	138.4	258.5	196.4
Lodgepole pine per ha, 1985	85.0	209.3	160.6
Lodgepole pine mean dbh, 1985	20.3	21.8	28.4
2002 to 2008 mountain pine beetle outbreak			
BA, 2002 (all species, $m^2\,ha^{-1}$)	12.1	12.2	32.0
Trees per ha, 2002 (all species)	259.3	339.7	674.4
Lodgepole pine killed (%)	32.6	48.4	58.0
BA, 2008 (all species, $m^2\,ha^{-1}$)	9.5	6.5	12.3
Trees per ha, 2008 (all species)	208.6	184.9	296.3
Lodgepole pine per ha, 2008	80.3	153.8	164.2
Lodgepole pine mean dbh, 2008	16.8	19.8	22.4

Notes: Data for 1981 are from Cole *et al.* (1983), data for 1985 from Amman *et al.* (1988), and 2002–2008 data from the present study. Different untreated stands were measured in 1985 and 2002–2008; untreated stand comparisons across the intervals are not recommended. Also, different subsets of the original diameter-limit cutting units (Cole *et al.* 1983) were measured by Amman *et al.* (1988) and the present study and caution is advised when comparing stand characteristics across the intervals.

Large diameter pines are most favored by mountain pine beetle (Cole and Amman 1969, Amman *et al.* 1977), and a goal of the original diameter-limit cutting treatments was to reduce susceptibility by removing all large (> 18- or 25-cm dbh) lodgepole pines. In 2002, 22 years after the diameter-limit treatments, average lodgepole pine dbh in cutting treatments was less than in untreated reference stands, and also less than it was five years post-treatment, the latter likely due to ingrowth. Total stand density and pine density were also less in the cutting treatments relative to reference stands. The original prescription goal of fewer large and less dense host trees, which contributed to reduced mountain pine beetle-caused tree mortality five years post-treatment, continued to provide reduced tree mortality after nearly 30 years. In 2002, diameter-limit cuttings were well below density levels considered susceptible to a mountain pine beetle outbreak (i.e., 27.5 $m^2\,ha^{-1}$; Mata *et al.* 2003), and significantly fewer pines were killed by mountain pine beetle relative to reference stands. These results suggest that diameter-limit cutting treatments to 18 and 25 cm did not reach a high level of susceptibility 22–28 years post-treatment.

Despite the significantly reduced mountain pine beetle-caused tree mortality among treated stands, 28 years post-treatment and after two mountain pine beetle outbreaks, the treated and untreated reference stands had similar lodgepole pine density (≥ 12.7 cm dbh; Fig. 3). This result is similar to that from a retroactive study of partial cutting in spruce to reduce losses to spruce beetle. Thinned spruce stands, with treatment ages up to 20 or more years before infestation, had significantly lower mortality rates compared to untreated stands, yet untreated stands had more residual live, mature spruce (Hansen *et al.* 2010). Mountain pine beetles act as natural thinning agents, albeit residual spacing is likely to be different than that from cultural treatments, resulting in similar post-treatment densities in thinned and untreated stands.

Although Amman *et al.* (1988) reported increased lodgepole pine recruitment in diameter-limit cutting treatments five years post-treatment, we found no differences in lodgepole pine regeneration among the untreated reference and treated stands 28 years post-treatment. In cutting treatments, however, we observed an increase in lodgepole pine tree density (≥ 12.7 cm dbh) and a decrease in mean dbh from five to 22 years post-treatment. These results suggest that the regeneration measured by Amman *et al.* (1988) grew into the 12.7 cm class by the time of our surveys. A predominance of serotiny in the study area, poor seedbed conditions, or reduced seed availability due to removal of high proportions of mature trees could explain a lack of continued recruitment in the more open, heavily cut stands relative to reference stands (Lotan 1976). Prescriptions often require additional stand entries, which did not occur at our study site. Pre-commercial thinning of non-pine species, in conjunction with planting, could be used to increase lodgepole pine regeneration (Lotan and Perry 1983), particularly in the 18-cm thin stands. The low density of 0-cm class lodgepole pine seedlings relative to non-pines in both partially cut and reference stands suggests that the stands will trend away from lodgepole pine dominance in the long-term, barring fire or mechanical treatment. Mountain pine beetle outbreaks, however, are typically followed by a pulse of lodgepole pine recruitment into canopy gaps (Hansen 2014). Thus, recurring outbreaks can slow or hasten the conversion to shade-tolerant species depending on the species composition of advance regeneration and recruitment.

Another caveat regarding our results is that some small amount of mountain pine beetle-caused tree mortality likely occurred following our 2008–2009 surveys. NIDDS maps indicated that the mountain pine beetle epidemic phase, which generally lasts about six years (Cole and Amman 1980), began by 2002 in the study area and then dropped off substantially in 2009 with the last record of activity in 2010. Our surveys were conducted near the end of the epidemic phase, although they may not fully reflect conditions at the end of the outbreak.

Conclusion

A variety of thinning strategies have been tested for reducing mountain pine beetle-caused tree mortality (Fettig *et al.* 2014). In most cases, reduced stand density associated with thinning is assumed to result in changes to microclimate, tree

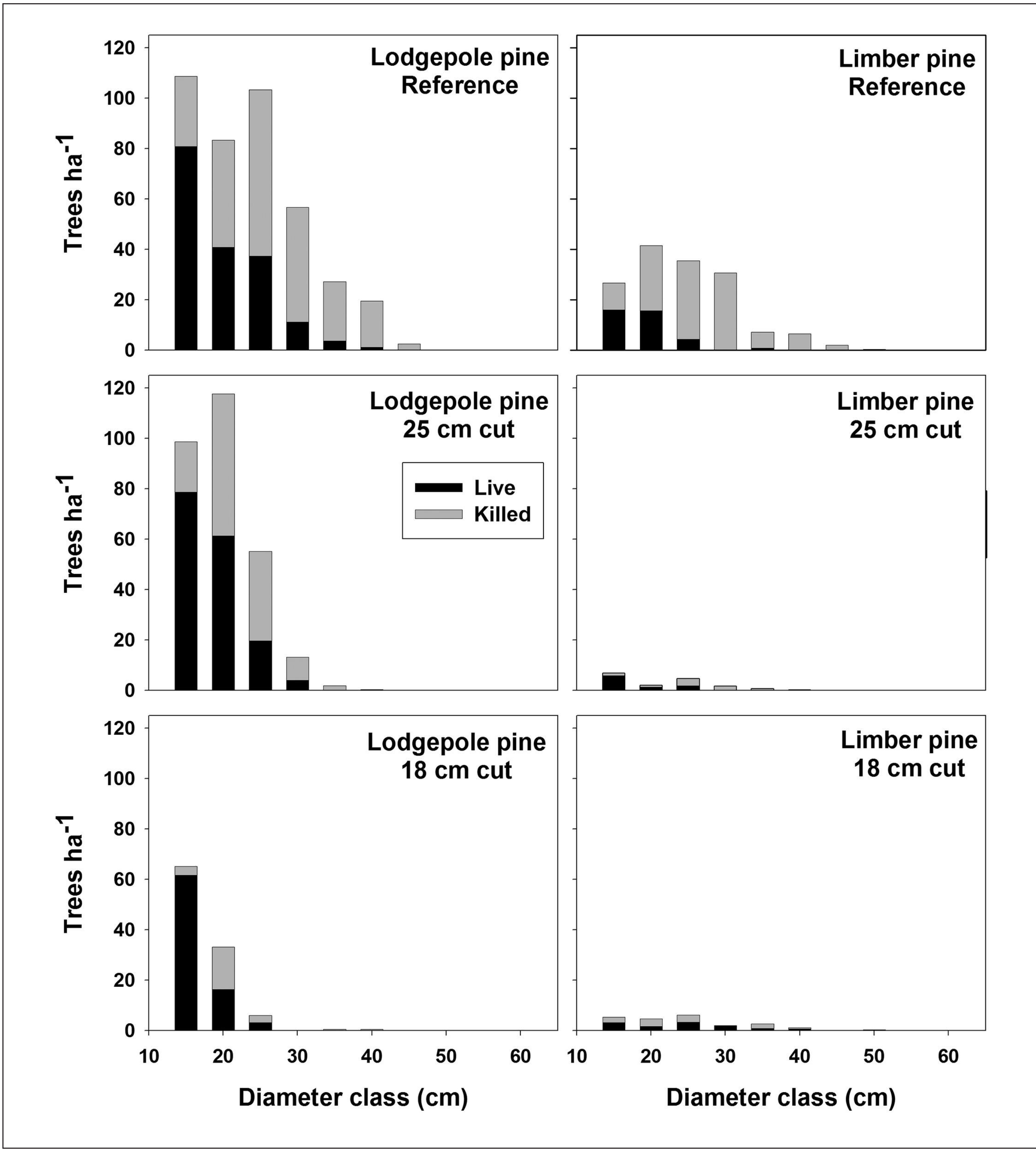


Fig. 5. Densities of live and beetle-killed lodgepole and limber pine by size class, among diameter-limit cutting treatments and untreated reference stands in 2008, 28 years after partial cutting treatments and after mountain pine beetle outbreaks in 1981–1985 and 2002–2008. Thinning from above, to 18 or 25 cm dbh (lodgepole pine only) was conducted 1979–1981. Data are averaged from variable radius plots from stands on the Shoshone National Forest, Wyoming.

spacing, and host vigor that inhibit beetle population success, and diameter-limit cuts from above also remove the pines most susceptible to beetle infestation. Although thinning from below is currently preferred on public lands, diameter-limit cuts are still common on private lands (Gillette *et al.* 2014). We found that, nearly 30 years post-treatment, stands treated with diameter-limit cuts remained less susceptible to mountain pine beetle than untreated reference stands. Despite the reduced beetle-caused mortality, however, residual live mature lodgepole pine density was similar in partially cut and untreated reference stands; there was no benefit to long-term lodgepole pine regeneration from partial cutting, and mean lodgepole pine dbh was greater in reference stands. Moreover, following an outbreak 22 years post-treatment, the 18-cm cuts had no lodgepole pine in diameter classes ≥ 30 cm. The effect of recurring outbreaks seems likely to hinder pines from growing into the larger size classes, particularly in the diameter-limit cuts relative to reference stands. At the time of the original diameter-limit cuttings treatments, the management objective was to reduce mountain pine beetle-caused tree mortality, and this goal was achieved during outbreaks one to five years and 22 to 28 years after treatment. Additionally, mechanical removal of live trees: 1) provided wood products; 2) removed susceptible trees that, if infested, could subsequently contribute to increased surface fuel loadings and, potentially, more severe fire behavior (Page and Jenkins 2007, Klutsch *et al.* 2009); and, 3) facilitated road access for recreationists and further management. Other thinning options to reduce losses to mountain pine beetle in lodgepole pine include thinning from below and thinning to uniform residual spacing while clearcutting is another indirect control alternative (Fettig *et al*. 2014). Each of these cultural practices has advantages and disadvantages regarding efficacy against beetle infestation, economic viability, and residual stand conditions. The short- and long-term costs and benefits of diameter-limit cutting, including its effects on stand structure, should be considered when formulating management plans.

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Supplementary material

Table S1. Characteristics of individual stands surveyed in 2008–2009, 28 years after diameter-limit cutting from above to 18 cm and 25 cm dbh (lodgepole pine only), and following extensive mountain pine beetle-caused tree mortality between 2002 and 2008.

			Tree density (Trees ha^{-1})		Basal area (m^2 ha^{-1})		Live lodgepole pine (cm dbh)		Live limber pine (cm dbh)	
Treatment	Stand size (ha)	No. plots	2002	2008	2002	2008	2002	2008	2002	2008
Reference - 1	2.2	5	799	495	24	11	19.2	17.1	13.5	13.5
Reference - 2	5.0	10	671	275	37	12	24.9	21.6	29.2	19.7
Reference - 3	8.7	10	657	214	32	8	23.9	20.6	24.0	21.4
Reference - 4	5.8	10	633	300	35	14	27.8	23.3	23.7	17.9
18 cm cut - 1	22.6	11	407	383	23	20	20.3	20.7	28.5	27.1
18 cm cut - 2	11.1	12	395	342	19	16	17.6	16.5	32.5	32.0
18 cm cut - 3	11.1	10	423	295	19	14	18.9	19.9	35.7	33.0
18 cm cut - 4	26.3	12	235	233	13	13	17.4	16.5	35.1	35.1
18 cm cut - 5	10.2	12	328	161	13	6	17.9	15.8	23.4	21.2
18 cm cut - 6	7.3	10	275	171	11	7	17.8	16.3	*n/a*	*n/a*
18 cm cut - 7	23.9	12	63	63	2	2	15.8	15.8	20.3	20.3
18 cm cut - 8	17.0	24	142	136	4	4	14.9	14.8	25.4	24.1
18 cm cut - 9	19.0	16	234	193	5	4	15.6	14.9	19.4	*n/a*
25 cm cut - 1	6.5	10	351	132	12	4	20.0	18.3	26.2	26.2
25 cm cut - 2	12.9	15	305	158	9	4	19.3	18.2	22.6	22.6
25 cm cut - 3	3.1	6	243	144	10	6	20.0	19.0	*n/a*	*n/a*
25 cm cut - 4	8.2	10	400	231	13	6	18.8	17.2	21.2	16.8
25 cm cut - 5	6.9	8	430	246	15	7	20.1	19.4	*n/a*	*n/a*
25 cm cut - 6	3.1	5	360	175	14	6	20.8	19.1	22.0	19.6
25 cm cut - 7	12.3	10	256	123	14	9	20.2	20.0	20.3	15.7
25 cm cut - 8	5.2	8	388	265	13	8	19.8	18.3	26.2	26.2
25 cm cut - 9	25.3	17	291	169	10	4	18.9	16.2	22.1	13.7
25 cm cut - 10	7.1	9	270	96	10	3	20.7	18.9	20.7	24.9
25 cm cut - 11	46.2	11	473	305	14	8	18.9	17.7	*n/a*	*n/a*

Notes: Stand conditions in 2002 were estimated from 2008 data by recoding recently-killed trees as live. "No. plots" is the number of variable radius plots (10 ft^2 acre^{-1} BA factor) established for describing stand conditions. Mean tree density and basal area are for all tree species.

Table S2. Results of tests for differences among diameter-limit cutting treatments and untreated reference stands, 28 years after treatments, in the proportion of lodgepole pine and limber pine attacked and killed by mountain pine beetle between 2002–2008.

	Lodgepole pine		Limber pine	
	t-value$_{(df)}$	p(t)	t-value$_{(df)}$	p(t)
Stems infested				
25 cm vs 18 cm cuts	$1.70_{(21)}$	0.2286	$-0.85_{(18)}$	0.6780
25 cm vs reference	$-2.66_{(21)}$	0.0374	$-7.54_{(18)}$	< 0.0001
18 cm vs reference	$-3.50_{(21)}$	0.0058	$-7.08_{(18)}$	< 0.0001
BA infested				
25 cm vs 18 cm cuts	$0.62_{(21)}$	0.8133	$1.63_{(18)}$	0.2594
25 cm vs reference	$-2.88_{(21)}$	0.0235	$-4.64_{(18)}$	0.0002
18 cm vs reference	$-2.43_{(21)}$	0.0596	$-5.83_{(18)}$	< 0.0001

Notes: Diameter-limit cuttings from above, to 25 cm and 18 cm dbh, were conducted in 1979–1981 and resurveys for mountain pine beetle-caused tree mortality were conducted in 2008–2009. Generalized mixed model analyses were conducted using two metrics, the proportion of stems infested and the proportion of basal area (BA) infested. The numerator was derived using data from 20.1 m wide strip cruises (*i.e.*, population of beetle-killed pines) and the denominator was calculated from variable radius plot data (*i.e.*, the total pine population).

Table S3. Test results comparing live residual conditions, for stems ≥ 12.7 cm dbh, in 2008 among diameter-limit cutting treatments (25 cm and 18 cm, lodgepole pine only) and untreated reference stands 28 years after cutting partial treatments and following extensive beetle-caused mortality.

Species and treatment	$t\text{-value}_{(df)}$	X^2	$p(t; X^2)$
Live stem density			
Lodgepole pine			
25 cm vs 18 cm cuts	$2.84_{(21)}$	*n/a*	0.0256
25 cm cuts vs reference	$0.09_{(21)}$	*n/a*	0.9954
18 cm cuts vs reference	$-2.03_{(21)}$	*n/a*	0.1290
Limber pine			
25 cm vs 18 cm cuts	*n/a*	0.03	0.8641
25 cm cuts vs reference	*n/a*	40.10	< 0.0001
18 cm cuts vs reference	*n/a*	40.31	< 0.0001
Non-pine species			
25 cm vs 18 cm cuts	*n/a*	175.09	< 0.0001
25 cm cuts vs reference	*n/a*	101.49	< 0.0001
18 cm cuts vs reference	*n/a*	0.05	0.8311
Basal Area			
Lodgepole pine			
25 cm vs 18 cm cuts	$4.13_{(21)}$	*n/a*	0.0013
25 cm cuts vs reference	$-0.57_{(21)}$	*n/a*	0.8357
18 cm cuts vs reference	$-3.64_{(21)}$	*n/a*	0.0041
Limber pine			
25 cm vs 18 cm cuts	$-2.87_{(16)}$	*n/a*	0.0239
25 cm cuts vs reference	$-3.66_{(21)}$	*n/a*	0.0040
18 cm cuts vs reference	$-1.22_{(16)}$	*n/a*	0.4536
Non-pine species			
25 cm vs 18 cm cuts	*n/a*	74.30	< 0.0001
25 cm cuts vs reference	*n/a*	41.50	< 0.0001
18 cm cuts vs reference	*n/a*	0.01	0.9259

Notes: Diameter-limit cuts were conducted from 1979 to 1981. Density (trees ha^{-1}) and BA ($m^2\ ha^{-1}$) data are from variable radius plots (Table S1). Results are shown for mountain pine beetle host species (lodgepole and limber pine) as well as combined non-pine species (subalpine fir, Engelmann spruce, quaking aspen and Douglas-fir). Test results reported with t-values were conducted with generalized linear mixed models, whereas test results reported with X^2 statistics were conducted with zero-inflated Poisson regression models. The latter models were used in cases where the response variable had multiple zero observations (*e.g.*, stem density of relatively uncommon species such as limber pine), for which generalized linear mixed models resulted in poor residual distributions.

Table S4. Test results comparing lodgepole pine, limber pine, and non-pine regeneration density in three diameter classes (0 cm, 5 cm, 10 cm) 28 years after diameter-limit cutting treatments from above to 25 cm and 18 cm dbh (lodgepole pine only) and following extensive beetle-caused pine mortality from 2002–2008.

Species and treatment	t-value (df = 21)	Standardized test statistic	P
0 cm diameter class			
Lodgepole pine			
25 cm vs 18 cm cuts	-0.16	*n/a*	0.9862
25 cm cuts vs reference	-0.09	*n/a*	0.9951
18 cm cuts vs reference	0.03	*n/a*	0.9996
Limber pine			
25 cm vs 18 cm cuts	*n/a*	-3.8694	0.7849
25 cm cuts vs reference	*n/a*	-3.8694	0.0044
18 cm cuts vs reference	*n/a*	-3.8694	0.0224
Non-pine species			
25 cm vs 18 cm cuts	-0.41	*n/a*	0.9136
25 cm cuts vs reference	-0.33	*n/a*	0.9407
18 cm cuts vs reference	-0.02	*n/a*	0.9998
5 cm diameter class			
Lodgepole pine			
25 cm vs 18 cm cuts	-0.17	*n/a*	0.9841
25 cm cuts vs reference	2.07	*n/a*	0.1195
18 cm cuts vs reference	2.14	*n/a*	0.1052
Limber pine			
25 cm vs 18 cm cuts	*n/a*	-3.9122	0.0022
25 cm cuts vs reference	*n/a*	-3.9122	0.1092
18 cm cuts vs reference	*n/a*	-3.9122	0.2322
Non-pine species			
25 cm vs 18 cm cuts	-2.42	*n/a*	0.0619
25 cm cuts vs reference	-1.47	*n/a*	0.3249
18 cm cuts vs reference	0.38	*n/a*	0.9238
10 cm diameter class			
Lodgepole pine			
25 cm vs 18 cm cuts	-0.58	*n/a*	0.8333
25 cm cuts vs reference	1.22	*n/a*	0.4558
18 cm cuts vs reference	1.62	*n/a*	0.2615
Limber pine			
25 cm vs 18 cm cuts	*n/a*	-0.4310	0.2614
25 cm cuts vs reference	*n/a*	-0.4310	0.2614
18 cm cuts vs reference	*n/a*	-0.4310	0.2614
Non-pine species			
25 cm vs 18 cm cuts	*n/a*	-2.7437	0.0053
25 cm cuts vs reference	*n/a*	-2.7437	0.0571
18 cm cuts vs reference	*n/a*	-2.7437	0.5594

Notes: Cutting treatments occurred 1979-1981 and were re-surveyed in 2008. Non-pine species are subalpine fir, Engelmann spruce, quaking aspen and Douglas-fir. Test results reported with t-values were conducted with generalized linear mixed models whereas test results reported with standardized test statistics (overall model) were conducted with the non-parametric Multi-Response Permutation Procedure (Euclidean distance). The latter models were used in cases where the response variable had multiple zero observations (*e.g.*, stem density of relatively uncommon species such as limber pine), yet a zero-inflated Poisson regression models failed to converge.