



Tree mortality after synchronized forest insect outbreaks: Effects of tree species, bole diameter, and cutting history



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ABSTRACT

A recent series of bark beetle outbreaks in the Rocky Mountain region of the U.S. is the largest and most intense ever recorded. Factors contributing to tree mortality from bark beetles are complex, but include aspects of forest stand condition. Because stand conditions respond to forest management, evaluating bark beetle-caused tree mortality and changes in forest structural attributes in areas previously subjected to management not only improves mechanistic understanding of beetle-caused changes in forests, but also improves prediction of future bark beetle responses to management regimes. We retrospectively assessed mortality of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), and stand structure in two watersheds in south-central Wyoming, U.S.A. following outbreaks of mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*), and western balsam beetle (*Dryocoetes confusus*). One watershed received 240 patch cuts (mean area 1.5 ha), a type of group selection cut, six years before the beetle outbreaks began; the other watershed received no active management (control). We conducted surveys of forest vegetation attributes over 27 yrs, during pre-harvest, post-harvest, and post-outbreak periods. After the outbreak, lodgepole pine and Engelmann spruce mortality increased with increasing bole diameters and basal area of each species, but patterns of mortality were influenced by patch-cutting. Large-diameter trees in or near patch cuts tended to escape attack by bark beetles. Away from patch cuts (≥ 15 m), mortality of smaller lodgepole pine was higher compared to the control watershed. Based on our observed patterns of tree mortality, we hypothesize a changing pattern of host selection (i.e., selection for smaller trees) was influenced by stand conditions that created more suitable conditions for bark beetles in areas between patch cuts in the treated watershed. Snag density increased from pre-harvest to post-outbreak periods, but log density was similar, suggesting most dead trees remained standing at the time of data collection. Canopy cover did not decrease as expected, and ground cover did not change substantially from pre-harvest to post-outbreak periods. Patch-cutting improved survival probability of large-diameter lodgepole pine and Engelmann spruce during outbreaks of multiple species of bark beetle, although reduced losses were only realized for trees in or near (≤ 15 m) patch cuts. However, during intense, broad-scale tree mortality events, these benefits may be important in reducing the loss of mature trees to bark beetles and promoting retention of a larger cohort of mature trees post-outbreak.

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1. Introduction

Bark beetles, a group of species naturally occurring in coniferous forests of North America, are an important source of habitat modification and heterogeneity in these ecosystems (Schowalter

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et al., 1981; Franklin et al., 2007). Bark beetle outbreaks, under certain conditions, can result in high tree mortality over extensive areas, leading to cascading changes in structure or species composition of forests (Veblen et al., 1991). Outbreaks can also affect nutrient cycling and hydrologic processes, including water quality (Coulson and Stephen, 2006). Forest vertebrates can also be affected, via changes in resource availability or habitat selection (Martin et al., 2006; Saab et al., 2013). Specifically, insectivores may experience short-term surges in food availability, canopy-sensitive species may be negatively affected a few years after tree

death, and species associated with abundant logs may find favorable conditions 1–3 decades following the infestation. Beetle-caused tree mortality presents major management challenges in terms of fire risk, hazard trees, and timber production (Samman and Logan, 2000). These challenges may result in significant economic consequences due to altered forest management prioritizing trail and road clearing, or changes in wood fiber characteristics affecting potential wood products for many decades. Therefore, studies of the magnitudes of beetle infestations relative to host species, tree size and cutting history are needed.

During the past two decades conifer forests in the Rocky Mountains experienced one of the most intense and extensive beetle-caused tree mortality events ever recorded. Forests of nearly every coniferous type from New Mexico to British Columbia have been affected. Multiple species of bark beetle have been involved. In Colorado and Wyoming, the primary species have been mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) and spruce beetle (*Dendroctonus rufipennis* Kirby), and to a lesser extent, western balsam beetle (*Dryocoetes confusus* Swaine; Raffa et al., 2008; Bentz et al., 2009). A disturbance of this magnitude necessarily motivates a broad range of ecological and management questions related to bark beetles. These beetle species largely kill individual trees within mature forest stands at low rates during most years but extensive forest mortality events, like that observed recently in the Rockies, occur episodically (Raffa et al., 2008). Except during the most severe outbreaks, small trees are rarely attacked or killed by these species of bark beetles (Bleiker et al., 2003; Fettig et al., 2007). For instance, MPB attack lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) trees <10 cm diameter at breast height (dbh; Roe and Amman, 1970; Shore et al., 2006) at much lower rates than larger trees, demonstrating the influence of individual tree characteristics on bark beetle activity. However, the susceptibility of individual trees >10 cm dbh may differ as a function of stand condition, topography, elevation, tree vigor, weather, and climate, at local and regional scales. Stands with greater tree density or basal area have been shown to be at greater risk of attack by beetles, and risk of attack increases with stand age, percentage of host type, and in stands with a high proportion of large diameter trees (Christiansen et al., 1987; Fettig et al., 2013). Otherwise susceptible stands may resist attack and suffer low tree mortality during years of above-average precipitation indicating the importance of climate in broad-scale mortality events (Chapman et al., 2012; Raffa et al., 2008). Furthermore, brief weather events can have dramatic influence on tree mortality – extreme winter cold that extends over several weeks may significantly reduce beetle-caused tree mortality for several years (Macias Fauria and Johnson, 2009).

Partial cutting in systems dominated by lodgepole pine and ponderosa pine (*P. ponderosae* Dougl. Ex Laws.) has effectively reduced mortality rates from MPB (MacGregor et al., 1987; Amman et al., 1988; Schmid and Mata, 2005). Similarly, mortality from spruce beetles was significantly reduced in stands of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) treated with partial-cutting (Hansen et al., 2010). Therefore, partial cutting has emerged as a potential tool for reducing total tree mortality in landscapes at risk for infestation. However, the efficacy of partial cutting in reducing bark beetle-caused mortality may be influenced by remaining levels of growing stock, patterns of tree grouping, stand structure, and landscape context, as well as beetle demography and behavior (Olsen et al., 1996; Schmid and Mata, 2005; Fettig et al., 2007). Structural characteristics in post-harvest stands can influence microclimate, which is perhaps even more important than structural characteristics *per se* because it strongly affects beetle behavior and whether a suitable host tree is attacked (Bartos and Amman, 1989). In managed stands, bark beetles may be deterred by microclimate features such as warmer temperatures, lower humidity, and higher wind speeds than in unmanaged

stands. These factors may inhibit larval development or the spread of pheromone plumes used to coordinate tree attacks with other individuals (Amman and Logan, 1998; Thistle et al., 2004). Thus, an evaluation of specific partial cutting techniques is essential to determine how overall tree mortality rates may be affected.

Beginning in approximately 1996, MPB populations erupted in north-central Colorado and south-central Wyoming (Harris et al., 2001). Since approximately 2005, MPB populations have been at epidemic levels in mountains of southern Wyoming (Harris, 2006). As of 2012, over 1.7 million ha of pine (*Pinus* spp.) – dominated forests in south-central Wyoming and Colorado had been affected by this series of outbreaks (Harris, 2013). Additional outbreaks of other bark beetle species occurred concurrently with the initial MPB outbreak. Spruce beetle activity began with a large blowdown event in 1997 near Steamboat Springs, Colorado. As of 2012, spruce beetles had affected >420,000 ha in south-central Wyoming and Colorado. In the same region, western balsam bark beetle, a species implicated in mortality of subalpine fir, had affected >95,000 ha (Harris et al., 2001, USDA Forest Service, <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/>).

The occurrence of these bark beetle outbreaks in two watersheds where pre-outbreak data on forest structure and composition were collected presented the opportunity to evaluate whether patch-cutting, a type of group selection cut, influenced subsequent tree mortality or stand structure. Our objectives were to compare changes in tree mortality and structural attributes over time between patch-cut and uncut stands in treatment and control watersheds. We also tested for the previously demonstrated relationship between basal area and mortality rate of the same species. We include pre-epidemic data to evaluate whether changes in forest characteristics caused by the beetle epidemic were affected by forest management.

2. Materials and methods

2.1. Study site

Our study was conducted in the Sierra Madre Mountains of south-central Wyoming, in the Medicine Bow National Forest near the town of Encampment. Mean annual temperature during the period 1982–1986 was estimated to be 1 °C, and ranges from –10 °C in January to 12.9 °C in July. Mean annual precipitation is 87 cm, about 70% of which falls as snow (Bevinger and Troendle, 1987).

The study site comprised the Coon Creek and adjacent East Fork, Encampment River (“East Fork”) watersheds (Fig. 1). These watersheds were the site of a water yield augmentation project, begun in 1985 and completed in the 1990s, designed to evaluate the efficacy of one timber harvest technique to increase surface water yield at the scale of large basins (Troendle et al., 2001). Paired watersheds covering 1673 ha (Coon Creek) and 908 ha (East Fork) were selected based on similar size, aspect, elevation, and timber cover. Mean aspect for Coon Creek is 266° and for East Fork is 197°, and elevation for both watersheds ranges between 2682 and 3322 m (Troendle et al., 2001). During 1990–1992, 240 small patch cuts (mean area 1.5 ha; range: 0.1–7.0 ha) were created in Coon Creek while East Fork remained untreated. Within Coon Creek, a 985-ha portion considered to be the sampling area received 155 patch cuts and a system of access roads (total length = 31.5 km). Within patch cuts, most trees >15 cm dbh were removed, leaving fewer than 10 trees/ha (Hayward et al., 1999). Some advanced regeneration was retained, but as much as 95% of volume was removed. Patch cuts were distributed uniformly throughout the treated area, resulting in cut areas that were 53 m from the nearest neighbor, on average (Troendle et al., 2001). Prior to harvest, both watersheds

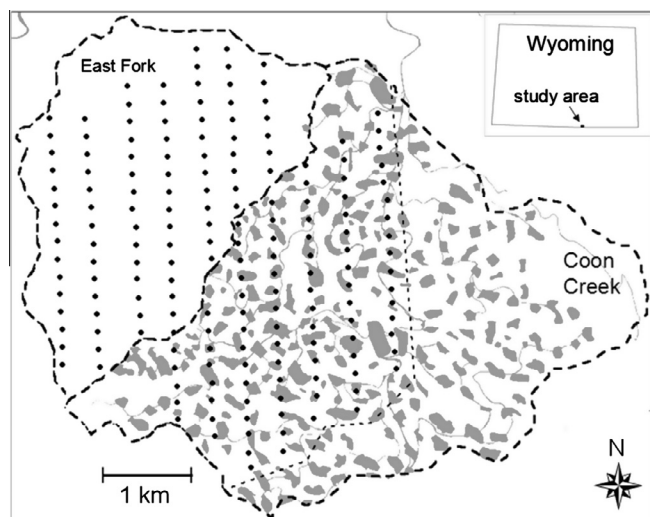


Fig. 1. Watershed boundaries (thick dashed line) for the control (East Fork) and treatment (Coon Creek) watersheds and location of 180 plots used for vegetation surveys (black dots) in south-central Wyoming, USA. Plots are 200 m apart along north–south transects, and transects are 400 m apart. The thin dashed line delineates the portion of the treatment watershed that was sampled during vegetation surveys. Dark gray areas indicate patch cuts and roads.

were dominated by lodgepole pine (60%) and Engelmann spruce-subalpine fir (40%) cover types, and 70% of the forest was categorized as mature (Raphael, 1988). About 3.2% of the areas of both watersheds were natural openings; after harvest, 23% of the treatment watershed (22% of the sampled area) was in patch cuts. Cuts occurring in spruce–fir were smaller than those in lodgepole pine to allow for site protection, and all uncut areas were at least as large as cut areas. Cover types were cut in similar proportions to those available (χ^2 Goodness of fit = 5.2, d.f. = 4, $P = 0.26$), and 70% of the patch cuts occurred in areas dominated by lodgepole pine that was >41 cm dbh (USFS E. O'Doherty, unpublished data).

Foliage color and retention can be used as a coarse indicator of length of time since beetle attack, and thus the approximate stage of the beetle epidemic (Safranyik et al., 1974; Klutsch et al., 2009). In both watersheds in 2011, 43% of all lodgepole pine had green foliage (indicating the tree was still alive), 7% had red foliage (indicating the tree was attacked within the last 2 yrs), and 49% of trees were gray (indicating the tree was attacked >2 yrs prior and most foliage had fallen off). Fifty-four percent of all Engelmann spruce had green foliage, <1% had red or yellow foliage, and 46% were gray. Seventy-one percent of subalpine fir had green foliage, <2% had red foliage, and 27% were gray (Johnson and Buskirk, unpublished data). Color assessments were made visually in the field. The low proportion of lodgepole pine in the red phase and high proportion in the gray phase suggest mountain pine beetle activity may have been largely completed in these two watersheds by 2011. Additionally, mountain pine beetle populations were reported to have declined locally, impacting fewer acres in south-central Wyoming in 2012 than 2011 (Harris, 2013). Spruce beetle activity was also likely complete in our watersheds given our observed patterns of foliage color, and aerial survey reports that spruce beetle activity decreased from 2011 to 2012 on the Medicine Bow National Forest. Western balsam bark beetle activity was considered moderate, but increased from 2011 to 2012 (Harris, 2013, USDA Forest Service, <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/>).

2.2. Data collection

In each watershed, 90 permanent sampling points were systematically placed from a random start at 200-m intervals along

north–south transects 400 m apart (Fig. 1). Sampling points were established prior to any harvesting activities. Vegetation surveys were conducted at sampling points in 1985 (pre-harvest), 1992 (post-harvest), 2011, and 2012 (both years representing post-outbreak conditions). Observers measured a distance of 11.3 m and 15 m from each point in four cardinal directions and marked the boundaries of the plot with survey flags. In the treatment watershed observers recorded whether any part of the 15-m plot fell within a patch cut; if so, the plot was designated a “patch-cut” plot; if not the plot was designated an “uncut” plot. All plots within the control watershed were designated as “control” plots. All vegetation data were collected within the boundaries of the 11.3-m-radius (0.04-ha) plot. Because sampling point locations were designated before cutting took place, part of the 0.04-ha plots designated as “patch-cut” often included portions that were not cut, but laid adjacent to a cut (Fig. 1).

In 1985, 1992, and 2011, cover percentages were estimated visually for shrubs, grasses/sedges (“grasses”), and forbs. Number of snags (trees that were dead and ≥ 20 cm dbh and ≥ 2 m tall) and logs (≥ 20 cm diameter at 1.5 m from large end, ≥ 2 m long, and $\geq 10\%$ within the 0.04-ha plot) were counted. Canopy cover was estimated using the average of one reading taken in each cardinal direction at the boundary of each plot using a spherical densiometer. Basal area for each tree species was estimated using a metric relascope in 1985 and 1992, and using a wedge prism relascope in 2011.

In 2012, observers used the same 0.04-ha plots to refine estimates of tree mortality by species and size class. All trees >1.4 m tall were counted, identified to species, assigned to one of nine size classes (≤ 10 , 11–15, 16–20, 21–30, 31–40, 41–50, 51–60, 61–70, or ≥ 71 cm dbh), and assigned a status of live or dead. Live trees were identified as having a canopy mostly comprised of green foliage; dead trees were identified as those not meeting the green foliage requirement and within any stage of decomposition but still standing.

2.3. Statistical analysis

Mortality rates for each tree species were compared using mixed effects analysis of variance in Program SAS (V. 9.3), where treatment (control, treatment uncut, and treatment cut) was modeled as a fixed categorical effect, total basal area of each species was modeled as a fixed continuous effect, and individual plot was a random effect. We also tested for effects of treatment $\times$ total basal area to address the question of whether the effect of total basal area differed depending on proximity to timber harvest. We evaluated changes in vegetation characteristics over time using mixed effects repeated measures analysis of variance with year as the repeated variable. Covariance structure for measurements among time periods was initially unknown, and our five candidate models included: compound symmetry, unstructured, autoregressive, heterogeneous autoregressive, and autoregressive moving average covariance structures. We calculated the most appropriate model covariance structure and improved model fit by comparing models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson, 2002). Response variables were transformed when necessary to meet assumptions of normality and homogeneity of variance. We used Tukey's method to control for Type I error probability when making multiple comparisons among control, uncut, and patch-cut plots for stand structure variables. However, formal hypothesis testing of all possible pairwise comparisons of tree mortality that included all nine size classes would have resulted in an adjusted alpha-level that was too restrictive. Thus, for tree mortality rates we compared degree of overlap of 95% confidence intervals among treatments within a size class to identify which size class categories drove differences

among treatments. The probability that a tree was dead in each size class and treatment was estimated using logistic regression, where size class was treated as an ordinal variable. A Wald test was then used to test the significance of treatment variables. Means are presented $\pm$ standard error.

3. Results

3.1. Tree mortality

For lodgepole pine, average mortality rate ranged from 3% for trees <10 cm dbh in patch cuts to nearly 100% for trees >30 cm dbh in either watershed (Fig. 2). Lodgepole pine mortality for all size classes pooled differed among treatments ($F = 27.65_{2,176}$, $P < 0.0001$). Mortality was similar between control ($42.7 \pm 2.8\%$) and uncut plots ($36.7 \pm 3.9\%$), but was lower in patch-cut ($11.7 \pm 4.2\%$) compared to control ($t = 6.08$, $P < 0.0001$) and uncut plots ($t = 4.27$, $P < 0.0001$). Differences in lodgepole pine mortality among treatments reflected lower mortality for trees ≤ 10 cm dbh in patch cuts than in control and uncut plots, as well as for trees 21–30 cm dbh compared to uncut plots (Fig. 2). While the pattern of lower mortality in patch cuts did not hold for trees 31–40 cm dbh, variation was high for mortality in this size class in patch cuts. However, mortality was 0% for pines in the largest size classes (51–70 cm dbh) in patch cuts. Total basal area (expressed as m^2 per 0.04 ha) of lodgepole pine affected mortality rate ($F = 16.82_{1,176}$, $P < 0.0001$); the relationship was positive ($\beta = 0.01$, $t = 4.10$, $P < 0.0001$; Fig. 3). This relationship was similar across treatments. The probability of a lodgepole pine dying depended on size class and treatment, but generally increased with tree size ($\chi^2 = 72.5$, d.f. = 2, $P < 0.0001$; Table 1).

For Engelmann spruce, mortality rates varied from 2% for trees <10 cm dbh to near 100% for trees >40 cm dbh in both watersheds (Fig. 2). Spruce mortality for all size classes pooled differed among treatments ($F = 22.57_{2,176}$, $P < 0.0001$). Mortality was similar between control ($27.9 \pm 2.3\%$) and uncut plots ($23.0 \pm 3.2\%$), but was lower in patch cut ($9.5 \pm 3.5\%$) compared to both control ($t = 4.38$, $P < 0.0001$) and uncut plots ($t = 2.79$, $P = 0.02$). Total basal area of Engelmann spruce affected mortality rate ($F = 53.70_{1,176}$, $P < 0.0001$), and the relationship was positive ($\beta = 0.03$, $t = 7.33$, $P < 0.0001$; Fig. 3). This relationship was similar across treatments. The probability of an Engelmann spruce dying depended on size class and treatment, but generally increased with size ($\chi^2 = 26.1$, d.f. = 2, $P < 0.0001$; Table 1).

In the case of subalpine fir, average mortality varied from 6% for trees <10 cm dbh in uncut plots of the treatment watershed, approaching 40% for trees >40 cm dbh in the control watershed (Fig. 2). However, mortality was generally lower for trees >40 cm dbh than for lodgepole pine or Engelmann spruce. Although overall mortality differed among treatments ($F = 3.53_{2,176}$, $P = 0.03$), mortality was similar among control ($11.3 \pm 1.6\%$), uncut ($17.0 \pm 2.2\%$), and patch cut ($12.1 \pm 2.4\%$) plots after adjustments for multiple pairwise comparisons. Total basal area of subalpine fir affected mortality rate ($F = 35.66_{1,176}$, $P < 0.0001$) and the relationship was positive ($\beta = 0.02$, $t = 5.97$, $P < 0.0001$; Fig. 3). This relationship was similar across treatments. The probability of a subalpine fir dying was similar among size classes and treatments ($\chi^2 = 1.8$, d.f. = 2, $P = 0.40$).

Mean snag density (for all species combined) depended on year and treatment (year $\times$ treatment interaction: $F = 22.57_{4,177}$, $P < 0.0001$; Table 2). In control plots, snag density was similar pre-harvest to post-harvest, but was higher post-outbreak compared to both pre-harvest (mean difference: 5.5 ± 0.5 snags; $t = 10.94$, $P < 0.0001$) and post-harvest (mean difference: 5.0 ± 0.5 snags; $t = 9.57$, $P < 0.0001$). In the treatment watershed, snag

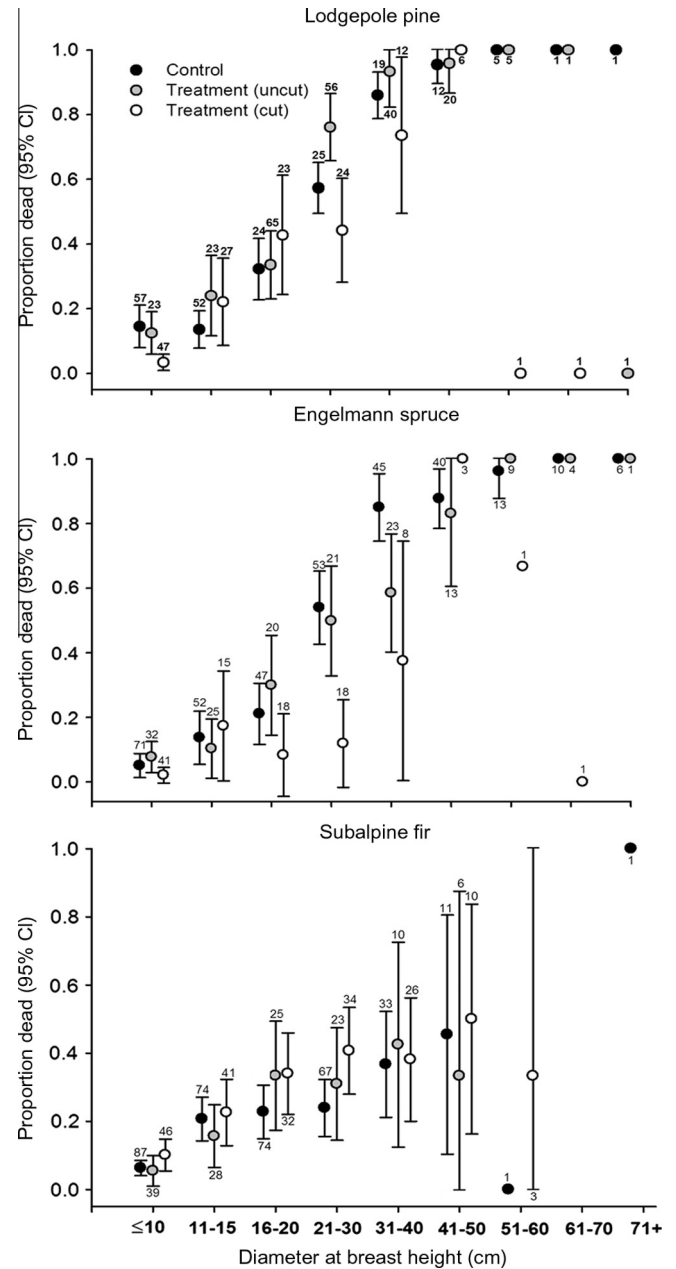


Fig. 2. Lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) mortality by size class and patch cutting treatment (control: sampling points located in the control watershed; treatment [uncut]: sampling points located between patch cuts in the treatment watershed; treatment [cut]: sampling points with any part of the 0.04-ha plot located within a patch cut in the treatment watershed). Error bars are 95% confidence intervals and numbers above or below data point indicate number of sampling points with trees in the respective size class. Data are from two watersheds in the Sierra Madre Range, south-central Wyoming, USA.

density in uncut plots was similar between pre-harvest and post-harvest, but was higher post-outbreak compared to both pre-harvest (mean difference: 6.1 ± 0.7 snags; $t = 9.55$, $P < 0.0001$) and post-harvest (mean difference: 5.9 ± 0.7 snags; $t = 8.79$, $P < 0.0001$). In cut plots, snag density was similar between pre-harvest and post-harvest and between pre-harvest and post-outbreak, but was lower post-outbreak than post-harvest (mean difference: 1.0 ± 0.8 snags; $t = -3.21$, $P = 0.04$).

Canopy cover depended on year and treatment (year $\times$ treatment interaction: $F = 47.36_{4,177}$, $P < 0.0001$; Table 2). In control plots, canopy cover was similar between pre-harvest and post-harvest, but

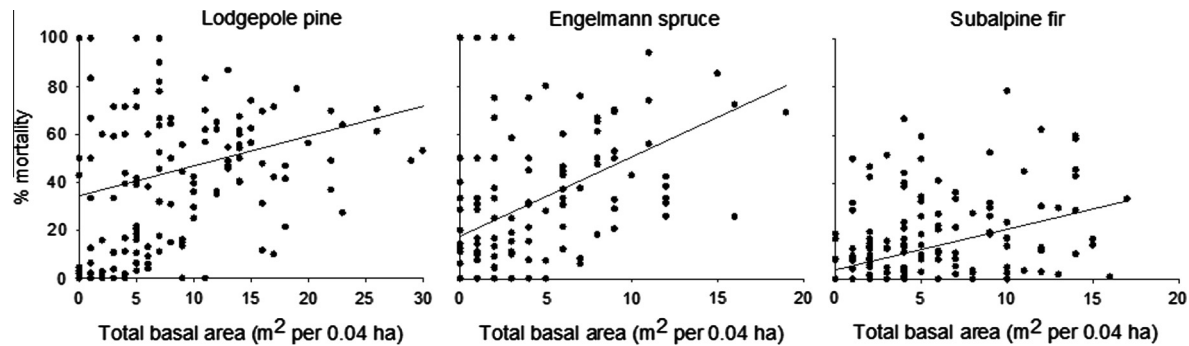


Fig. 3. Mortality rates of three tree species in relation to total (live and dead) respective basal area in south-central Wyoming. Lines represent predicted values from a mixed model with fixed effects of total basal area and treatment, and a random effect of sampling plot. Points where total basal area = 0 but mortality > 0% represent sampling artifacts: basal area (BA) was estimated using a wedge prism relascope and where trees were few, BA was estimated as 0. However, mortality rates were estimated by counting all stems within a plot, so trees that were excluded while measuring BA were included in mortality counts.

Table 1
Probability of mortality (95% confidence intervals) for subalpine forest after a broad-scale bark beetle outbreak in the Sierra Madre range, south-central Wyoming. Size classes are based on diameter at breast height (dbh). Trees > 60 cm dbh were encountered too infrequently to include in our analysis; however, mortality for this size class approached 100% (Fig. 2). Size class/treatment/species categories too sparsely encountered to allow estimation of probabilities of mortality are indicated by “–”.

Treatment	Size class (cm)	Probability of mortality		
		Lodgepole pine	Engelmann spruce	Subalpine fir
Control	≤10	0.13 (0.10–0.15)	0.04 (0.03–0.07)	0.07 (0.05–0.08)
Control	11–15	0.20 (0.15–0.25)	0.13 (0.08–0.19)	0.19 (0.16–0.23)
Control	16–20	0.35 (0.29–0.41)	0.30 (0.22–0.40)	0.28 (0.24–0.34)
Control	21–30	0.64 (0.59–0.68)	0.59 (0.52–0.66)	0.28 (0.23–0.33)
Control	31–40	0.89 (0.83–0.93)	0.90 (0.83–0.95)	0.37 (0.27–0.48)
Control	41–50	0.96 (0.88–0.99)	0.90 (0.82–0.95)	0.45 (0.25–0.66)
Control	51–60	–	0.95 (0.73–0.99)	–
Patch cut	≤10	0.01 (0.00–0.02)	0.02 (0.01–0.06)	0.04 (0.03–0.06)
Patch cut	11–15	0.22 (0.14–0.31)	0.14 (0.07–0.26)	0.28 (0.21–0.37)
Patch cut	16–20	0.50 (0.40–0.60)	0.06 (0.01–0.20)	0.15 (0.09–0.25)
Patch cut	21–30	0.62 (0.53–0.70)	0.11 (0.04–0.27)	0.20 (0.11–0.34)
Patch cut	31–40	0.79 (0.67–0.88)	0.41 (0.21–0.65)	0.57 (0.23–0.86)
Patch cut	41–50	–	–	–
Patch cut	51–60	–	0.67 (0.15–0.96)	–
Uncut	≤10	0.16 (0.12–0.20)	0.11 (0.08–0.19)	0.09 (0.07–0.11)
Uncut	11–15	0.24 (0.19–0.30)	0.21 (0.14–0.30)	0.30 (0.25–0.36)
Uncut	16–20	0.43 (0.37–0.50)	0.34 (0.24–0.45)	0.38 (0.30–0.47)
Uncut	21–30	0.74 (0.69–0.79)	0.54 (0.44–0.63)	0.45 (0.37–0.53)
Uncut	31–40	0.96 (0.89–0.99)	0.64 (0.51–0.75)	0.46 (0.32–0.61)
Uncut	41–50	0.94 (0.69–0.99)	0.82 (0.57–0.94)	0.40 (0.16–0.70)
Uncut	51–60	–	–	–

increased by $21.5 \pm 2.3\%$ from pre-harvest to post-outbreak ($t = 6.59$, $P < 0.0001$) and by $23.4 \pm 1.5\%$ from post-harvest to post-outbreak ($t = 10.19$, $P < 0.0001$). In the treatment watershed, canopy cover in uncut plots was similar from pre-harvest to post-harvest, but increased by $17.7 \pm 3.0\%$ between pre-harvest and post-outbreak ($t = 3.35$, $P = 0.03$) and by $19.7 \pm 2.8\%$ from post-harvest to post-outbreak ($t = 4.56$, $P < 0.001$). In cut plots, canopy cover decreased by $65.4 \pm 3.0\%$ from pre-harvest to post-harvest ($t = -15.31$, $P < 0.0001$), and by $42.2 \pm 3.3\%$ from pre-harvest to post-outbreak ($t = -8.87$, $P < 0.0001$), but increased by $65.8 \pm 2.3\%$ from post-harvest to post-outbreak ($t = 7.16$, $P < 0.0001$).

3.2. Ground cover

Log density (mean number of logs per 0.04-ha plot) depended on year and treatment (year $\times$ treatment interaction: $F = 6.24_{4,177}$, $P = 0.0001$). In control plots, log density decreased by an average of 5.1 ± 0.7 from pre-harvest to post-harvest ($t = -7.44$, $P < 0.0001$) and by an average of 5.3 ± 0.7 between pre-harvest and post-outbreak ($t = -7.51$, $P < 0.0001$; Table 2). In the treatment watershed, log density in uncut plots decreased by 9.3 ± 0.9 from pre-harvest to post-harvest ($t = -10.18$, $P < 0.0001$)

and by 9.0 ± 1.0 from pre-harvest to post-outbreak ($t = -9.43$, $P < 0.0001$), post-harvest to post-outbreak. In cut plots, log density decreased by an average of 8.5 ± 1.0 from pre-harvest to post-harvest ($t = -8.29$, $P < 0.0001$) and by 10.3 ± 1.1 from pre-harvest to post-outbreak ($t = -9.65$, $P < 0.0001$). Log density was similar between post-harvest and post-outbreak for all plot types, demonstrating that most dead trees resulting from the beetle epidemic were still standing at the time of data collection.

Percent shrub cover depended on year and treatment (year $\times$ treatment interaction: $F = 15.32_{4,177}$, $P < 0.0001$). In control plots, shrub cover was similar among all three time periods (Table 2). In the treatment watershed, shrub cover decreased in uncut plots by $16.7 \pm 2.5\%$ from pre-harvest to post-harvest ($t = -6.76$, $P < 0.0001$), was similar between pre-harvest and post-outbreak, and increased by $18.0 \pm 2.5\%$ from post-harvest to post-outbreak ($t = 7.13$, $P < 0.0001$). In cut plots, shrub cover decreased by $23.4 \pm 2.8\%$ from pre-harvest to post-harvest ($t = -8.50$, $P < 0.0001$) and by $17.6 \pm 2.6\%$ from pre-harvest to post-outbreak ($t = -6.69$, $P < 0.0001$), but remained similar between post-harvest and post-outbreak. Percent forb cover depended on year and treatment (year $\times$ treatment interaction: $F = 16.57_{4,177}$, $P < 0.001$). In control plots, forb cover was similar

Table 2

Mean (95% confidence intervals) values for vegetation attributes at 0.04-ha plots in subalpine forest stands during three time periods (pre-harvest = 1985; post-harvest = 1992; post-outbreak = 2011) in south-central Wyoming, USA.

	1985			1992			2011	
	Control	Treatment	Control	Treatment (uncut)	Treatment (cut)	Control	Treatment (uncut)	Treatment (cut)
Snag density	2.0 (1.6–2.5)	1.9 (1.5–2.3)	2.5 (1.9–3.1)	2.6 (1.7–3.4)	2.4 (1.7–3.0)	7.5 (6.5–8.5)	8.4 (7.3–9.4)	0.9 (0.4–1.4)
Log density	10.8 (9.5–12.2)	15.9 (14.1–17.6)	2.5 (2.0–4.1)	3.0 (1.5–3.7)	8.0 (6.1–9.9)	7.5 (6.3–9.0)	8.3 (5.1–9.8)	6.4 (4.8–7.9)
Canopy cover	65 (61–69)	68 (64–71)	64 (60–67)	69 (65–73)	24 (19–30)	79 (76–81)	78 (74–81)	39 (33–46)
Percent shrub cover	46.4 (41.6–51.3)	47.7 (42.6–52.9)	40.9 (36.6–45.3)	28.3 (22.7–33.8)	26.7 (22.1–31.3)	42.0 (36.9–47.0)	46.0 (39.0–52.4)	32.9 (27.4–38.5)
Percent forb cover	10.8 (7.3–14.3)	9.5 (5.5–13.4)	8.1 (5.9–10.3)	7.7 (4.3–11.1)	1.4 (1.1–1.8)	8.3 (6.0–10.5)	10.6 (6.9–14.4)	7.8 (6.2–9.4)
Percent grass cover	13.1 (8.5–17.8)	8.5 (4.4–12.6)	11.2 (7.4–15.0)	8.0 (3.6–12.4)	2.3 (1.0–3.7)	13.4 (9.9–16.9)	11.3 (6.6–16.0)	14.9 (10.2–19.5)
Percent total vegetation cover	64.4 (60.5–68.2)	61.7 (57.1–66.2)	60.2 (57.2–63.3)	43.9 (37.5–50.4)	30.4 (25.9–35.0)	63.6 (60.0–67.2)	67.5 (62.5–72.5)	55.6 (50.5–60.7)
Percent lodgepole pine ^a	49.0 (42.4–55.7)	54.3 (46.9–61.6)	46.4 (39.9–52.9)	46.5 (35.9–57.1)	41.9 (31.7–52.1)	44.0 (37.1–50.1)	48.1 (37.2–59.0)	41.1 (28.8–53.4)
Percent Engelmann spruce ^a	24.7 (19.4–30.1)	21.2 (16.1–26.4)	24.4 (19.2–29.6)	26.1 (18.7–33.6)	14.4 (8.3–20.5)	22.1 (17.1–27.1)	25.9 (18.5–33.2)	19.5 (11.0–28.0)
Percent subalpine fir ^a	26.2 (22.1–30.3)	24.5 (20.2–28.9)	29.2 (25.0–33.4)	27.4 (21.2–33.7)	34.4 (25.8–43.0)	32.9 (28.1–37.7)	25.7 (19.1–32.2)	31.9 (22.6–41.2)

^a Percent of total basal area (live + dead) for each species.

among years. In the treatment watershed, forb cover in uncut plots was similar from pre-harvest to post-harvest and from pre-harvest to post-outbreak, but increased by 3.3% between post-harvest and post-outbreak ($t = 4.72$, $P < 0.0001$). In cut plots, forb cover was similar from pre-harvest to post-harvest, but increased by 4.7% from pre-harvest to post-outbreak ($t = 6.83$, $P < 0.0001$), and by 6.4% from post-harvest to post-outbreak ($t = 10.06$, $P < 0.0001$; Table 2). Percent grass cover depended on year and treatment (year $\times$ treatment interaction: $F = 15.63_{4,177}$, $P < 0.0001$). In control plots, grass cover was similar between pre-harvest and post-harvest and pre-harvest and post-outbreak, but increased by $2.2 \pm 1.2\%$ from post-harvest to post-outbreak ($t = 3.21$, $P = 0.04$). In the treatment watershed, grass cover in uncut plots was similar between pre-harvest to post-harvest and pre-harvest and post-outbreak, but increased by $3.6 \pm 1.6\%$ from post-harvest to post-outbreak ($t = 3.16$, $P = 0.05$). In cut plots, grass cover was similar from pre-harvest to post-harvest, but increased by $12.9 \pm 2.2\%$ from pre-harvest to post-outbreak ($t = 10.28$, $P < 0.0001$) and increased by $13.0 \pm 1.8\%$ from post-harvest to post-outbreak ($t = 9.93$, $P < 0.0001$).

Total vegetation ground cover (shrub + forb + grass cover) depended on year and treatment (year $\times$ treatment interaction: $F = 20.33_{4,177}$, $P < 0.0001$). In control plots, total vegetation cover was similar among all years. In the treatment watershed, total vegetation cover in uncut plots decreased by $23.4 \pm 2.5\%$ from pre-harvest to post-harvest ($t = -9.44$, $P < 0.0001$), increased by $24.8 \pm 2.5\%$ from post-harvest to post-outbreak ($t = 9.93$, $P < 0.0001$), but was similar between pre-harvest and post-outbreak (Table 2). In cut plots, total vegetation cover decreased by $25.8 \pm 2.8\%$ from pre-harvest to post-harvest ($t = -9.37$, $P < 0.0001$), and increased by $25.3 \pm 2.8\%$ from post-harvest to post-outbreak ($t = 9.09$, $P < 0.0001$). Total vegetation cover was similar between pre-harvest and post-outbreak in uncut and cut plots.

4. Discussion

Tree mortality patterns after recent synchronized bark beetle outbreaks were influenced by tree species, bole diameter, and cutting history. Mortality was highest for lodgepole pine and Engelmann spruce, while subalpine fir experienced generally lower mortality. Mean mortality rates tended to increase with size class and basal area for lodgepole pine and Engelmann spruce, but varied widely for subalpine fir in larger size classes. At the lowest

values of basal area, mortality rate of subalpine fir was less than 10%. Surprisingly, canopy cover increased, and coarse woody debris remained similar from pre-outbreak to post-outbreak time periods. Ground vegetation cover did not change markedly from pre-outbreak to post-outbreak time periods, with the exception that grass cover increased in patch cuts.

A potential limitation of our study is that we did not identify specific agents of tree mortality. However, attributing tree mortality to specific causes was not the primary focus of our study. Given the size and intensity of the ongoing bark beetle epidemic in the region and patterns we assessed while making field observations, we are comfortable assuming a relatively large proportion of tree mortality was caused by bark beetles. However, we emphasize that this report is of the status of Rocky Mountain subalpine forest before and after a major bark beetle event that occurred across the region, but our patterns of tree mortality reflect the results of multiple threats occurring coincidentally. Furthermore, these patterns of tree mortality associated with historical management have been retrospectively assessed. The study design did not originally include questions regarding beetle-induced tree mortality, thus providing limited potential to infer which processes produced the patterns we observed.

Higher mortality of larger trees is expected during outbreaks of mountain pine beetle, spruce beetle, and western balsam beetle, because larger trees are preferentially attacked by these species (Schmid and Frye, 1976; Geiszler and Gara, 1978; Bleiker et al., 2003). However, cutting history at our study site influenced mortality rates in unexpected ways. In patch cuts, mortality of lodgepole pine tended to be lower for several size classes than in uncut areas of the treatment watershed or the control watershed, suggesting patch cutting may benefit trees located close (≤ 15 m) to cuts during bark beetle outbreaks. Indeed, in patch cuts, trees in the largest size classes had no mortality (Fig. 2). Uncut areas between patch cuts in the treatment watershed (>15 m away from a patch cut) generally had similar mortality rates for lodgepole pine as the control watershed for all size classes pooled, but evaluating patterns within each size class reveals an exception for trees 21–30 cm dbh. Trees in this size class located between patch cuts experienced higher mortality than trees of similar size in the control watershed (Fig. 2). We hypothesize that this pattern reflects the effect of the spatial distribution of suitable and unsuitable conditions on bark beetle behavior in the treatment watershed. Bark beetle activity tends to be greater near trees with closed canopy where temperature, light intensity, and wind speed remain at optimum levels (Bartos and Amman, 1989), characteristics which are

likely met in uncut plots but less so in patch cuts. Further, host trees of preferred sizes are located closer to each other in uncut plots than in and around patch cuts, and thus may be easier for bark beetles to locate. When the first few individuals attack a tree, those individuals emit an aggregating pheromone that attracts other individuals to the same tree. Once the tree's defenses have been overcome, individuals emit a disaggregating pheromone which repels additional individuals (Raffa et al., 2008). Individuals repelled from the focal tree should attack suitable trees nearby, producing a clustering effect on mortality that has been shown in other studies (Preisler, 1993; Safranyik and Carroll, 2006; Progar et al., 2013). The patch cuts in the treatment watershed may have increased the patchiness of the microclimates suitable for beetle activity, and concentrated beetles in areas away from patch cuts, leading to higher mortality among slightly smaller trees in areas between patch cuts than in the control watershed. A similar pattern was not observed in the control watershed where suitable microclimates and host trees are more evenly distributed across the watershed.

Other investigators have observed comparable patterns in which tree selection by bark beetles varied over the course of an outbreak (Klein et al., 1978; Amman and Cole, 1983). In these studies, selection for smaller-diameter trees increased as the pool of large-diameter available host trees declined. Here we present evidence consistent with this changing pattern of host selection on a spatio-temporal scale. At our study site, some large-diameter host trees near patch cuts—trees of the size class that would have been preferred early in the outbreak—escaped attack by beetles, presumably because they were less likely to be encountered. We hypothesize that this occurred because the low density of large-diameter trees in patch cuts led to a lack of signals from beetles in the area that large trees were available. Thus, from a beetle's perspective, perceived host depletion may have occurred more quickly in areas near patch cuts, forcing beetles to select smaller host trees in areas farther from patch cuts with high mean densities of trees of suitable diameter.

Patterns of mortality for Engelmann spruce were generally similar to those for lodgepole pine, and trees in most size classes seemed to benefit from being located in or near patch cuts. Group tree selection methods, including patch-cutting, are commonly used to facilitate Engelmann spruce regeneration in the central Rockies. These methods result in stands with higher species and age-class diversity, which are less susceptible to direct bark beetle attack, but may also indirectly aid suitable hosts in avoiding attack by making them less obvious to beetles (Price, 1997; Fettig et al., 2007).

Patterns of mortality for subalpine fir differed from that of the other tree species studied. While the positive relationship with basal area was similar to other species, overall mortality was lower and did not differ among control, uncut, and patch cut plots. Further, the relationship between dbh and mortality was weak. Although initial attacks by western balsam bark beetles may not result in mortality, the beetles can introduce the fungus *Ceratocystis dryocetidis*, which can increase the susceptibility of the tree to subsequent beetle attacks, both of which may ultimately result in mortality (Molnar, 1965; Garbutt, 1992). Further, subalpine fir mortality in the region of our study area has been attributed to a combination of root disease caused by *Armillaria* spp. or *Heterobasidium* spp. and western balsam bark beetle activity, collectively known as “subalpine fir decline” (Harris et al., 2001; Harris, 2012). Limited data are available on bark beetle-caused mortality of true fir (Fettig et al., 2007), but studies by Bleiker et al. (2003) and McMillin et al. (2003) suggest that mortality patterns are similar to other tree species that host bark beetles: larger trees with reduced vigor are more susceptible to attack. However, because mortality often occurs in conjunction with other factors such as

blow-down events and root and fungal disease, mortality patterns of subalpine fir at our study site may reflect more complicated dynamics than just initial stand and tree conditions.

Although mortality rates differed slightly for some species and size classes, stand conditions following the outbreaks were similar between plots in the control watershed and uncut plots in the treatment watershed. Further, differences in stand conditions between patch-cut plots and control or uncut plots were largely restricted to snag and log density, and we found few substantial differences in ground cover by 10 yrs post-harvest. However, as more snags fall and coarse woody debris on the forest floor increases over time, important differences in ground cover between patch-cut and other treatments may become apparent.

Our observation of increased canopy cover from pre-outbreak to post-outbreak periods was unexpected. This result is likely a function of increased stand age over time, but may also reflect the use of a spherical densiometer to quantify canopy cover. We recognize the weaknesses associated with spherical densiometers (Cook et al., 1995). However, so that our data could be compared to historical data recorded at the study site, we opted to use the same method to measure canopy cover. Because most dead trees were still standing at the time of data collection, substantial decreases in canopy cover likely have not yet occurred. Although needle loss from the canopy has occurred, densiometers may not have the sensitivity required to capture such fine-scale changes in canopy cover.

5. Conclusions

Patch-cutting in subalpine forest appears to have improved survival probability among lodgepole pine and Engelmann spruce during a synchronized bark beetle outbreak, although reduced losses to bark beetles were only realized for trees in or near patch cuts. However, during intense, broad-scale events with mortality of some size classes approaching 100% like that occurring at our study site, these benefits may be important in reducing the loss of mature trees to bark beetles and promoting retention of a larger cohort of mature trees after the outbreak. Thus, patch-cutting executed under multiple forest management goals, including reducing bark beetle-caused mortality, should be considered as a measure offering partial protection from mortality within the context of the extent and intensity of the beetle outbreaks and proximity of focal trees to patch cuts.

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